DEPARTMENT OF APPLIED STATISTICS
UNIVERSITY OF LONDON, UNIVERSITY COLLEGE

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BIOMETRIC SERIES XII

ON THE SESAMOIDS OF THE KNEE-JOINT

(REPRINTED FROM *BIOMETRIKA* VOL. XIII, 1921)

BY
KARL PEARSON, F.R.S.
AND
ADELAIDE G. DAVIN, B.Sc.

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That in this one thing, all the discipline
Of manners and of manhood is contain'd;
A man to joine himselfe with th' Vniverse
In its main sway, and make (in all things fit)
One with that all, and goe on, round as it;
Not plucking from the whole his wretched part
And into straites, or into nought revert,
Wishing the compleate Vniverse might be
Subject to such a ragge of it as hee;
But to consider great Necessitie.

GEORGE CHAPMAN

PART I

MAN

ON THE SESAMOIDS OF THE KNEE-JOINT.

By KARL PEARSON AND ADELAIDE G. DAVIN.

PART I. MAN.

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(1) *Introductory.*

During the course of recent work* on the femur of the primates undertaken in the Biometric Laboratory, much material accumulated bearing on the sesamoids of the knee-joint. It was found impossible to incorporate this in that work itself, and as it was very largely due to a third investigator it is only fitting that the paper should be not only published separately, but with a different authorship. Some of those acquainted with the literature of the subject may consider that all that is necessary to be known on such an apparently small topic has been fully dealt with already in the voluminous memoirs of Gruber† and Pfitzner‡. Both of these memoirs have their individual excellences, but we still venture to think that they have no more exhausted the subject than we ourselves are likely to do. Indeed merely a résumé of their work in a form easily accessible to English readers would be of service; but we hope to have added at least something of value to it, having trusted to what we believe is the only safe method of research, namely the first-hand investigation of the phenomena themselves before starting any study of the observations and opinions of others§.

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* Pearson and Bell, *A Study of the Longbones of the English Skeleton.* Part II, The Femur of Man, with special reference to the Primate Femora, see p. 512. *Drapers' Company Research Memoirs*, Cambridge University Press.

† For the full title of Gruber's classical memoir (hereinafter cited merely as Gruber) see our p. 24.

‡ For the full title of Pfitzner's memoir (hereinafter cited merely as Pfitzner) see our p. 31.

§ Some time may be lost by postponing the study of the literature of a topic until at least a late stage of one's own researches, but on the other hand a preliminary study will too often check one's own individual line of research either by emphasising others' methods of approach, as if they were the sole roads to truth, or by crowding the mind with a mass of other people's details, often best described as debris.

Before we can properly talk about our subject it is really needful to have some terminology. The sesamoid may be a true ossification of hyaline cartilage, or it may be a thickening or nodule of cartilage without ossification. In the young it is open to us to consider the latter as a stage of growth towards the former. In the adult this is not possible. We can, of course, assert, as many anatomists have done, that all sesamoids are produced by intensive stress acting on cartilage, but we shall then have to account for the absence of sesamoids in regions where such stress undoubtedly exists. Or we may look upon the non-ossified nodule as an attempted sesamoid, or better still as a vestige or trace in the species of where a sesamoid once has been. Whatever account of the matter we choose to accept, it is needful to distinguish between the two cases. Pfitzner proposed to call the bone a *sesamum* and the nodule a *sesamoid*. This upsets the historic origin of the word, for the Greeks most probably knew only the *sesamum* and called it a *sesamoid*, and the name sesamoid remained as a name for the bone through many centuries. We might speak of sesamoid bone and sesamoid nodule or cartilaginous sesamoid, but the terms are cumbersome. We shall accordingly reserve the term sesamoid or *orthosesamoid* for a true bone and adopt an independent term for the thickened but unossified element of cartilage, calling it a *hemisesamoid*. Further we shall term all pathological ossifications, exostoses, or again, broken off and not reunited portions of bone occurring in or near the positions of sesamoids, *pseudosesamoids*.

In the knee-joint itself we have come across no less than ten sesamoids, some of which are, however, more frequent or better established than others. To these sesamoids we have given the following distinctive names:

We retain the names of lateral *fabella* and mesial *fabella* for the sesamoids found in the tendons of *M. gastrocnemius* above the lateral and mesial condyles respectively.

We introduce the term *cyamella** for the sesamoid which is to be found in the tendon of *M. popliteus*. It may be termed the *lateral cyamella* to distinguish it from a *mesial cyamella* which Pfitzner asserts he observed in two cats†. Gruber, notwithstanding his wide knowledge, seems to us to have confused the lateral *cyamella* in man with an unusual position of the lateral *fabella*. The existence in the cat of both lateral *fabella* and lateral *cyamella* ought to have warned him that both might appear in man.

Lastly a number of sesamoids occur in the borders of the semi-lunar cartilages. We term these *lunulae*‡. They may occur in six positions which we describe as follows: antero-lateral, antero-sagittal, antero-mesial, postero-lateral, postero-sagittal, and postero-mesial. Of these the sagittal are doubtful and may be anomalous in all species. Thus we have two *fabellae*, two *cyamellae* and possibly six *lunulae* as sesamoids of the knee-joint. In most cases some only of these will be present; in certain species some will always be present as true sesamoids, or will be present as

* *Cyamella*, a small bean, the bean-stone, an ornament worn by Roman women.

† Pfitzner, S. 584, without identification of an association with any particular muscle.

‡ *Lunula*, a little moon, a crescent, or crescent form of ornament worn by Roman women.

anomalies. In other species some will only appear as hemisesamoids; while in a third species, if they have been reported at all, it is probable that they were really pseudosesamoids.

Now to obtain a large number of knee-joints for dissection in the case of a particular species is practically impossible. In the case of dry material and skeletons the articulator may, perhaps generally does, preserve the *fabellae*, far more rarely the *cyamellae* or *lunulae**. Thus the actual presence of *cyamella* or *lunula* conveys definite information, their absence practically conveys nothing. It is extremely hard to demonstrate an invariable absence, especially in the case of an anomaly which may have a very small percentage of occurrences like the lateral *cyamella* in man. When one anatomist asserts the existence of a sesamoid which nine others deny, there is no grave difficulty in reconciling their statements, if the anomaly be present in only a small percentage of cases, and none of these anatomists have had the chance of examining more than a few individual cases of the species in question. This is, we think, the quite adequate explanation of the contradictions we find in the early history of the subject, and forms the chief difficulty in applying our analysis of the sesamoids of the knee-joint to the problems of evolution.

These problems are of the following character. Suppose we can classify those families in which certain sesamoids are (i) invariably present in the knee-joint, (ii) invariably absent, (iii) exist only as anomalies of a given order of rarity, will not such classifications throw light on evolutionary order? For example if we confine our attention to the primates, there are families in which the *fabellae* are both invariably present, others in which they are both invariably absent, others in which both are anomalous, and still another group in which the *fabella lateralis* is a true or orthosesamoid when it appears, and the *fabella mesialis* a hemisesamoid. Again the *cyamella lateralis* is invariable in certain monkeys, never appears in the gibbon, but is constant in the orang, and a rare anomaly in man. A similar series of statements can be made with regard to the presence or absence of *lunulae* in the primates. May it not be possible to throw light on primate evolution from such considerations?

The problems with regard to sesamoids are not only rendered difficult of solution by reason of the amount of material requisite for adequate classification, but by the longstanding existence of opinions and dogmas with regard to them.

The definition of the medical student that a sesamoid is any bone which it is unnecessary to study for examination purposes is, of course, an echo of the treatment of sesamoids in the current anatomical text-books, and that treatment has its historic evolution—broken only and for a short period by the discovery of the *fabellae* in man by Vesalius—from Galen to the present day; the text-book anatomists from his day through the centuries to our own have echoed his phrase as to sesamoids—that of those bones "which are termed sesamoids from their likeness to sesame" *non est necessarium hoc opere pertractare*[*]. If only Galen had told us which sesamoids he knew, what sesame was[†], and how and why they were like the seeds of it, our task would have been simplified! The comparison may have been obvious to the Greek anatomists because the sesame seed that they were referring to was familiar to their readers and because they had special sesamoid bones in mind, it is far less obvious nineteen centuries later.

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* In 15 dog skeletons in the Biometric Laboratory, the *fabellae* are almost invariable, the *cyamella* has not been preserved in a single case.

But we are not exact in stating that sesamoids have as a rule been dismissed in the language of Galen in the text-books. The opinion that it was unneedful to discuss them has been frequently accompanied by the dogma that sesamoids are the product of intensive stress acting upon cartilage. This dogma appeared to receive confirmation from the undoubted existence of hemisesamoids in regions where orthosesamoids are usually or on occasion discoverable. A hemisesamoid was an orthosesamoid in the making. This dogma appealed to that tendency in anatomy—largely the product of pathological study—which attributes innumerable characters of individual bones to specific use. The bone was not adapted by evolution to its use, but use was the source of its characters, and indeed if these were observed in the foetus or at birth, they were in themselves evidence of the inheritance of acquired characters. The *fossa hypotrochanterica* and the crural trough were the product of muscular action on the bone, even if they were to be found more frequently in female than male femora and were discoverable in infants and non-robust or even diseased bones. The "intensive stress" origin of sesamoids had indeed been questioned by Dr Robert Nesbit before the middle of the 18th century. He wrote as follows in his *Human Osteogeny*, London, 1736, p. 136:

"The only parts of a foetal skeleton, which remain to be taken notice of, are the *ossa sesamoidea* which all the writers, I have met with on this subject, have wholly passed over unobserved. The number of them in *foetuses* are, as in adults, very different in different subjects. Those, which are the most constantly found, are two in the bottom of the foot, fixt in the ligament of the articulation of the first bone of each great toe, with its *os metatarsi*. In all *foetuses*, from three months after conception to birth, the places of these *ossa sesamoidea* are always filled with cartilages of nearly the same shape those *sesamoide* bones usually have, when they are arrived at perfect maturity, *Plate* IV [actually Plate VI] *fig.* 18 *a. a. fig.* 19 *a. a.* In one subject at birth I found, in each of the *sesamoide* bones of one foot, a very small point of ossification.

"In like manner those *ossa sesamoidea* which are sometimes found at the beginning of the *musculi gastrocnemii*, are to be seen in *foetuses*.

"By the descriptions I have now given of all the different parts of foetal skeletons, it manifestly appears, that there is not one single bone, except the teeth, or one *epiphysis* in an adult skeleton, which is not to be found in a full grown *foetus*, or in its place a cartilage of nearly the same shape: consequently, the account cannot be right, which the ingenious professor *Monro* gives of the *ossa sesamoidea* being

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[*] *Liber de ossibus Galeni Librorum Pars Quinta*, Basileae, 1538, p. 727.

[†] See, however, below, p. 9.

'nothing else than the ligaments of the articulations, or the firm tendons of strong 'muscles, or both, become bony by the violent compression they suffer in the 'situation they are.'" (*Anatomy of the Bones*, Edinburgh, 1726, p. 337.)

It is true that this statement of Nesbit's, notwithstanding its definiteness and perspicacity, has been questioned somewhat cavalierly by Gruber*. He says that for many years he examined the cadavers of embryos in last month, of new-born children in considerable number and of several children one to seven years old, and never found in the tendons of *M. gastrocnemius* a *cartilago hyalina* or *fibro-cartilago*. He does not state the exact numbers and appears to hold that Nesbit asserted the existence of orthosesamoids, whereas Nesbit as we read him is speaking of prefigurations. Yet Gruber did himself find the hyaline cartilage elements in the tendons of puppies at birth where the *fabellae* later develop, and notes that the lateral ossifies first (at about six months)†. He does not state how many embryos and children he examined, and it is clear that as at least 90 °/₀ of adults exhibit no *fabellae*, it is quite conceivable that Nesbit may have found the prefigurations and Gruber not. But the fact that prefigurations are found in puppies and kittens, and the additional fact that not all sesamoids are associated with intensive stress while many regions of intensive stress are not associated with sesamoids‡ should be enough to dismiss this hypothesis, were it not that its supporters can appeal, as has been done in the case of femoral facets, to the principle that acquired characters are inherited, a haven ready for the supporters of production by use, and one where the difficulty of demonstrating a negative—other than by Occam's Razor methods—leaves them in comparative security.

Perhaps the most effective ejectant is the appeal, such as we hope to make in this paper, to the facts of the evolution of the sesamoids. Pfitzner, who was a strong opponent of the intensive stress hypothesis, not only cites Nesbit's results, but cites the case of the *Marsupialia*, and figures the Wombat, of which he writes:

> Wenn man annehmen müsste dass Gebilde von so reicher Formenentfaltung wie diese Epiperone (so möchte ich sie nennen) beim Wombat jederzeit als "Product entzündlicher Reizung" oder dergl. neu entstehen könnten, so würde man bald jede wissenschaftliche Bearbeitung des Skeletsystems als ein aussichtloses Unterfangen erklären müssen§.

The reader who wishes to appreciate the full force of Pfitzner's argument should examine our Plate V, Fig. 13. It seems unanswerable as far as the Marsupials are concerned. Can we look for any evolutionary links between Pfitzner's "Epiperone," the "parafibula" of the Marsupials, and the sesamoids of the knee-joint of higher types?

For Pfitzner the source of the sesamoids is the same as that of any other bone of the skeleton, i.e. the force of heredity‖. He distinguishes as we have seen between orthosesamoids ("sesambeine") and hemisesamoids ("sesamoide"); the latter he considers develop in fibrous cartilage ("faseriges Gewebe") and do not ossify*. Hemisesamoids are abortive sesamoids; we may term them vestiges of past phases of evolutionary development. Pfitzner does not, however, attempt to follow up the view here suggested by the examination of sesamoids in a large number of types other than man. Man is of course the subject of his paper, and the sesamoids of the knee-joint with which we are at present interested form only one element in his monograph.

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* Gruber, p. 13.

† Gruber, p. 57. We have ourselves found them, as well as the *cyamella lateralis*, prefigured in puppies at birth, and the two *fabellae* and the *cyamella* in kittens at birth.

‡ Why should man and the greater anthropoids have lost their *fabellae* while they are universal in the lesser apes? The "stress" has hardly disappeared.

§ Pfitzner, S. 586.

‖ Pfitzner, S. 535 and S. 563.

The keynote, however, of Pfitzner's suggestion that hemisesamoids are not necessarily orthosesamoids in the making, but may be the evolutionary debris of what have been orthosesamoids, vestiges of ossificatory centres where no ossification now sets in, is well worth bearing in mind. It is not incompatible with sesamoids appearing in regions of intensive stress, for it is possible that in such regions the sesamoid or its precursor would be of special value to the organism.

(2) *Origin of the term Sesamoid.*

The term sesamoid is not to be found in any author previous to Galen†, but he uses it in the sense of a word familiar to his readers. It is probable that Galen only knew the sesamoids of hand and foot. He does not directly refer to those of the knee-joint. Eustachius in 1564 argued that Galen must have dissected the human cadaver and not those of monkeys‡, because he does not refer to the *fabellae*, but as Galen clearly considered sesamoids of no great importance, he may simply have omitted reference to them. If he dissected carefully a considerable number of human bodies, it is singular that he should not have met with the *fabellae* occasionally, but the same criticism applies to all anatomical writers up to Vesalius (1555).

We have been able to discover four passages, three in the accepted, one in the spurious books of Galen, referring to sesamoids. We cite from the Latin translations.

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* This does not seem in accordance with Gruber's view (see our pp. 25 and 43), that sesamoids are invariably prefigured by hyaline and not fibrous cartilage.

† Galen was born at Pergamum A.D. 131. He went to Rome and was known to Marcus Aurelius. He died aged 70.

‡ "Admiratione denique obstupui, cur anatomiae instauratores, in secunda libri de hominis fabrica editione, ubi administrationem musculorum pedis docent, duo ossicula magnitudine ciceris describant, quae supra utrumque femoris tuberculum reperiuntur, qua nimirum primi duo pedem moventes oriuntur musculi: nam & si ea in simijs & in canibus semper occurrant, in hominibus tamen adeo raro inueniuntur, ut non modo (quod posteriores addiderunt) saepius alterum, nunc internum, nunc externum deficiat, uerum etiam ut plurimum utrumq: ipsorum desit, miraculum enim existimabo si duo simul occurrent, & non mediocri diligentiae ascribam, si post multorum cadaverum sectionem alterum illorum quis inveniat. ideo que tantum abest, ut aequum sit eiusmodi ossicula inter hominis partes numerare, ut etiam liceat suspicari ea a Galeno consulto fuisse pretermissa, indeque sumere argumentum tantum anatomicae artis praeceptorem homines non simias nobis descripsisse. Addo sine aliquo fructu laborare illos, qui commentitias quasdam utilitates horum ossiculorum confingunt: neque enim natura, quae provida est & omnium opportunitatum moderatrix, veretur ne in cruris directione principia paulo ante memoratum musculorum comprimantur & atterantur. Si enim hic esset eius scopus in illis conformandis multo magis in homine, quam in simia & cane reperirentur, quando horum uterque longe minus, quam homo tibiam ambulando extendit."

See Bartholomaeus Eustachius, *Opuscula Anatomica*, Venice, 1564, p. 180.

The first reference is in the *Liber de ossibus*, and contains the passage to which we have already referred:

> Quod si quod ossiculum alibi utpote in corde, in naso, in gutture, itemque in aliquo ex digitis, ut quae a sesami similitudine sesamoide vocant, aliudque ejus generis deprehenditur, non est necessarium hoc opere pertractare*.

It will be seen that while the name sesamoid bone is of very early origin, the existence of the *fabellae*, the first sesamoids of the knee-joint to be talked about, if known was not recorded until 1555 and then not accurately, not indeed before Eustachius.

The second passage occurs in the *De usu partium corporis humani*† and runs as follows:

> Nonum aliquis potuit hoc carpi os numerare, sed non est numeratum ab anatomicis, sicut nec aliquod eorum, quae σησαμοειδῆ, a sesami leguminis minuti specie, vocantur, quae multis manuum et pedum articulis natura ex abundanti velut auctarium circumponet securitatis gratia.

Another reference occurs in the *De usu partium*, Lib. III, Cap. viii, where Galen mentions the two metatarsial phalangeal sesamoids of the great toe. It runs as follows:

> Quinetiam ei parti plantae, que magno digito praeposita est, duo [ossa *or* sesamoidea?] videntur subjecta esse inferiori regione, veluti sustentacula quaedam & stabilamenta, ut prius os magni digiti praedictae plantae parti, omnino jam in terram defixae conjugatur, undique, opinor, huic parti pedis natura suppeditante securitatem, ceu multum laboraturae propter praepositam sibi concavitatem & velut fornicem ossium. [Basel edition, 1561, *Prima Classis*, p. 259.]

Neither the Latin translation, nor the original Greek [Basel edition, 1538, p. 397], use the term sesamoid. But the word *ossa* seems omitted. It is supplied in the French translation (*De l'usage des parties du corps humain*, Paris, 1659, p. 120).

Now it is probable that these were the special sesamoid bones of the Greek anatomists, and they are bean-like rather than irregular or even lens-shaped. It is difficult to find a resemblance in them to the seed of the existing forms of sesame, as the reader will see by examining our Plate I, Fig. 2.

It will be noted that these passages from the real writings of Galen make the comparison with the sesame directly and not with its seed. It is otherwise in our third passage taken from the section *De anatomia oris* of the *Liber de anatomia virorum* ascribed to Galen‡:

> Veniunt autem duo musculi ei ab additamentis sesaminis, id est quibusdam parvis ossiculis ad modum seminis sesami, et sunt supplementa spondylorum colli.

Thus in the earliest traces we have of sesamoids the name seems to have stood for any small bone of no recognised importance, which in some way was like sesame, a small species of pulse. The earlier references may, the later does indicate comparison to the seed of this plant. These passages have been followed by later anatomists, and in each case we are told that certain bones are termed sesamoids because they resemble the seed of the sesame. What they themselves meant by "sesame," or what the Greeks understood by sesame in Galen's time, seems rarely to have entered the minds of these writers! Through the courtesy of the Director of Kew Gardens we have received samples of *Sesamum indicum* or *orientale*, the sesame as at present known in the East. It is almost impossible to believe that the Greek anatomists, who at least were familiar with the sesamoids "ex digitis," could have called these after their resemblance to the seed of sesame as now known*.

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* *Galeni Librorum Pars Quinta*, Basileae, 1538, p. 727. We can hardly expect that Galen would have anticipated the great evolutionary importance which the "sesamoidea gutturis" would attain to in later ages!

† Liber II, Cap. xii, *Galeni Librorum Prima Classis*, Basileae, 1561, p. 248.

‡ Galen's *Works*, Basileae, 1561, p. 49 c.

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* The seed is crescent rather than lentil-shaped, and extremely small; only its coloration is in its favour. The most obvious sesamoids for the Greeks were the sesamoids of the big toe (see our Plate I, Fig. 2) and there is nothing really comparable between the seed and these bones. In size and shape, if less in coloration, they are remarkably like the seeds of *Ricinus*. We ventured to put our difficulties before the Director of the Royal Gardens, Kew, and he has most kindly sent us the following memorandum by Dr O. Stapf. It seems more than ever probable from this that Galen in his account of the plants was not speaking from personal experience, but following Theophrastus and Dioscorides. If the seed of the sesame was known to Galen he appears to have had rather a poor imagination for comparisons. Perhaps he was familiar with a variety having a much larger seed. The comparison would be excellent had the sesamoids first observed been the *lunulae* of the squirrel.

Dr Stapf's *Memorandum on Sesamum and Sesamoids.*

1. I have no doubt that the *SESAME* of Galen was *Sesamum indicum.* The Greeks knew it as far back as the days of Herodotus, and the Greeks of Asia Minor were probably quite familiar with it.

2. The history of the plant or drug mentioned by Greek writers under the name Σησαμοειδές has been shrouded in mystery from the earliest times. We meet with it first in one of the few fragments which have been preserved to us from the writings of Diocles of Karystos, the most prominent physician of the fourth century B.C., the "sectator Hippocratis quem Athenienses iuniorem Hippocratem vocarunt" (see Wellmann in *Festgabe f. Franz Susemihl*, 1898, S. 23). Διοκλῆς, says Erotianos in his Glossary of Hippocrates, οὕτω φησὶ καλεῖσθαι τὸν ἐν Ἀντικύρᾳ ἐλλέβορον—ἕτεροι δὲ πόαν τινὰ ἕτεραν (Wellmann, *l.c.* 26). Thus it seems the people of Anticyra, a town in Phokis reputed for its Hellebore cures, used the word as a synonym of ἐλλέβορος, whilst others applied it to another herb. Theophrastus (about 370—285 B.C.) somewhat later speaks of the fruit of the sesamoid Hellebore being administered by the people of Anticyra, adding in the way of explanation that the fruit is similar to sesame (οἱ ἐν Ἀντικύρᾳ τοῦ σησαμώδους ἐλλεβόρου διδόασιν ὅτι ὁ καρπὸς ὁμοῖος σησάμῳ, ed. Loeb, *Class. Libr.* with transl. by A. Hort, ii. 288); whilst in another place (*l.c.* 260) he says that the fruit of the Hellebore which at Anticyra is used as a purge contains the well-known σησαμώδης. Here then the conception of "sesamoides" as a part of Hellebore is quite unequivocal.

Pliny refers in two places to Sesamoides; but his account is confused. In the 22nd book, chap. 25, he introduces it after *Sesame* and contrasts it with it. Sesamoides, he says, has its name because it resembles Sesame, but its grain is bitter, its leaves are smaller and it grows in gravelly ground; but there is also another kind which grows in Anticyra and is called Anticyron by some and this has leaves like those of groundsel. The seeds of both are taken as a purgative and the latter kind has white Hellebore root added to enhance its action. He once more reverts to "Sesamoides" in the 25th book, chap. 5, where he says that the people of the island of Anticyra add Sesamoides to their Hellebore (the black Hellebore is meant) to render it safe to take. There are thus two kinds of Sesamoides indicated, just as in Diocles, the Anticyrian and another. The Anticyrian, however, is not any longer a Hellebore or part of a Hellebore, but a different plant with leaves like those of Groundsel, whilst the other is also a distinct plant but of a different kind. If we now turn to Dioscorides who has largely drawn on the same sources as Pliny, we find the two "Sesamoides" still more sharply divided as μέγας (lib. iv, chap. 149) and μικρόν (lib. iv, chap. 163; Wellmann, *Dioscor.* pp. 292 and 309). It is the greater Sesamoides that stands for Hellebore in Anticyra and is added to the white Hellebore in preparing the purgative. It is described as resembling Groundsel (ἠριγέρων) or Peganum, and as having large leaves, white flowers, a slender inefficacious root and bitter seeds similar to those of sesamum. The alternative Groundsel or Peganum is puzzling. It can clearly not be similar to both, but from Wellmann's annotations it appears

The natural thing appears to be to consult Galen himself as to what was the nature of the plant he termed sesame*. Galen in several passages refers to the sesame or to plants of a sesamoid nature. We will give here the references we have been able to discover. In his *De simplicum medicamentorum facultatibus*† we read:

Sesamon. Sesamon non panem in se continet viscosum et pingue; quare emplasticum est & emolliens ac modice calidum. Ejusdem facultatis est, quod ex eo conficitur oleum; et herbae quoque decoctum similem vim obtinet.

This is immediately followed by a description of the sesamoid plants‡.

Sesamoides. Sesamoides magnum, quod & anticyricos helleboros appellatum est, propterea videlicet quia semen eius ut helleborus purget; hoc & reliqua facultate helleboro simile est. Nam & in abstergendo, excalfaciendo, desiccandoque, similem illi vim obtinet.

Sesamoides album. Sesamoides albi semen nonnullum item acrem qualitatem continet; sed multum amarum est; excalfacit itaque, rumpit, extergit.

In Liber I, Cap. XXX, "De Sesamis et Erysimo" of the *De alimentorum facultatibus Libri tres*:

Sesami semen pingue est ideoque repositum celerrime fit oleosum; quamobrem eos, qui ipso

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that the words ἠριγέρωντι ἢ are missing in Oribasius' manuscript of Dioscorides, whilst the codices of Constantinople, Naples and Munich lack the words ἢ πηγάνῳ. The latter reading is supported by the figure in the Constantinopolitan Codex, which represents faithfully a specimen of *Senecio lividus*. This figure is very like that of ἠριγέρων in the same code, the latter being unmistakably *Senecio vulgaris*. Compared with this *S. lividus* has actually larger leaves, whilst it shares with it the white pappus (flower) and slender inefficacious root; on the other hand it is difficult to see where the resemblance of the "seeds" (achenes) with Sesame seeds comes in. Nor are the achenes of either *Senecio* likely to be physiologically active.

The lesser Sesamoides (also called White Sesamoides or Wild Sesam) is said to have stems a span high, leaves like those of κορωνόπους, but rougher and smaller and to bear on the tips of the stems heads of purplish flowers with a white centre and in them bitter yellowish seeds like sesam; the root is slender and the plant grows in rough places. Of this too there is a fair figure in the Constantinopolitan Codex which can be identified with *Dorycnium hirsutum*, whilst κορωνόπους with which it is compared is from the table in the same Codex *Lotus arnithopodioides*. The representation of the leaves of the lesser *Sesamoides* and the *Coronopus* in the figures of the Code is indeed very similar. The white "centre" may mean the pale pods, whilst the seeds might very roughly be compared with those of sesame. As in the case of ἠριγέρων it is difficult to understand how small doses of the seeds, mixed with honey, as prescribed, could have been very effective. At the same time it is true that *Dorycnium hirsutum* was at one time in use as Herba Loti anti-haemorrhoidalis. Thus the plant was not unknown in the old herbalists' shops; but it long ago disappeared from the market.

To summarize briefly, the name *Sesamoides* designated early different plants or drugs. One of them was identical with the Hellebore of Anticyra or at least with its fruit. The others were entirely different species, in Pliny's and Dioscorides' times *Senecio lividus* and *Dorycnium hirsutum*. As there is no doubt that the (black) Hellebore of Anticyra was *Helleborus cyclophyllus*, the comparison of its fruit (follicles) with that of Sesame was not very far fetched, however little the two plants have in common in other respects.

To me the question of *Sesamoides*, whether magnum or parvum, seems to be irrelevant as far as the problem of the sesamoid bones is concerned. The sesamoid bones of Galen were no doubt in shape similar to the seeds of *Sesamum indicum*, hence "sesamoid," quâ forma, whilst the latter were similar to the seeds of *Ricinus* in yielding a fat oil, that is "sesamoid," quâ usu. Their relation to the sesamoid bones on one side and the plants called Sesamoides on the other is therefore merely that of "tertium comparationis."

* Pfitzner, S. 520, appears to confuse the sesame with the two sesamoides.

† Basileae, 1561, Liber VIII, p. 122.

‡ *Opera*, Secunda Classis, Basileae, 1561, p. 29, Greek Edition, Basileae, 1538, p. 317.

> vescuntur celeriter implet; stomachumque subvertit, ac tarde concoquitur, pingueque corpori praebet alimentum. Liquet ergo, quod ventriculi partibus vigorem ac robur addere nequit, quemadmodum neque aliud quodvis pingue. Est autem crassi succi, ideoque non propere pervadit. Ipso aut solo non admodum vescuntur, sed cum melle crudo quas vulgo *σισαμίδας* vocant effingentes. Panibus etiam inspergitur*. Porro, quemadmodum milio panicum (quod etiam *μελίνης* diximus appellari) adsimile quidem quodammodo est, verum undequaque deterius; ad eundem modum & sesamo erysimum corporis substantia quodam pacto est affine, sed in cibo est insuavius, corporique alimentum parcius exhibit, praedictoque omnino est deterius. Caeterum utrumque temperamento est calidum, ob eamque causam sitem etiam excitat.

A further reference to Sesamoides occurs in Galen's commentary on Hippocrates' book *De victus ratione in morbis acutis*†.

> Sesamoides superiorem ventrem purgat sesquidrachmae pondere in oxymelete tritum et potui datum. Miscetur autem veratris ita ut tertiam efficiat partem. Nempe id hoc pacto minus suffocat.

Lastly in Galen's book *De substitutis medecinis*‡ we read that the substitute:

> "pro sesamo" is *Linisemen* (*λινόσπορος*), i.e. linseed, "pro sesamoide" is *Amaranthi expressio* (*ἀμαράντου πίεσμα*), "pro Linisemine" is *Fabae medulla.*

There can be small doubt that for Galen sesame was an emollient, *Sesamoides magnum* a purgative, and *Sesamoides album* an emetic. The plants and their seeds have so little real resemblance that it is not impossible that the oil-giving property was the source of their common name§.

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* Sesame cakes or puddings were known to Xenophon and Aristophanes.

† *Opera*, Basileae, 1561, Septima Classis, p. 296, com. III, cap. 123.

‡ *Opera*, Basileae, 1561, Quinta Classis, pp. 173—4. It is clear that Galen distinguished linseed definitely from sesame, although he notes the emollient properties of sesame. See also the *De alimentorum facultatibus*, Liber I, cap. xxxii.

§ On p. 295 of the *Rariorum Plantarum Historia* 1601 of Carolus Clusius are given cuts of *Sesamoides magnum Salmantic.* and *Sesamoides parvum Salmantic.*, which indicate what was the type of plant denoted by these names in the latter half of the sixteenth century. Dr Stapf has kindly examined Clusius' figures for us. He says they are excellent figures, that the *Sesamoides magnum* is *Silene Otites*, Sm. and that *Astrocarpus Clusii*, J. Gay, is drawn for *Sesamoides parvum.* He has further found figures of the two *Sesamoides* in the *Codex Vindobonensis* (± a. 500 A.D.). *Senecio lividus* is figured as *S. magnum* and *Dorycnium hirsutum* as *S. minus.* Thus in Galen's time, in 500 A.D. and at the end of the sixteenth century we find different plants named as Sesamoides, and neither of the sets of figures here referred to are in the least helpful in interpreting what Galen understood by these plants, nor do the seeds of these plants throw any additional light on the adoption of the word by the anatomists—they are not more like a sesamoid bone than sesame itself. Dr Stapf throws light on the matter in the following note: "I have also gathered much information with respect to the attempts made by the writers of the renaissance to explain the two Sesamoides of Dioscorides, and particularly their reference to species of *Reseda.* I thought there might have been some tradition linking up their interpretation with the classic writers. So far as the Arabic literature is available to me there does not seem to be any such connection, but I have not seen Ibn Baithar who I understand quotes from an Arab author. As far as I can see the interpretations of the herbalists were nothing but more or less ingenious guesses. The *Reseda* theory can be traced back to Luca Ghini who laid out and was in charge of the Botanic Garden at Pisa from 1544—1555. Amatus Lusitanicus (1554) also speaks of having been told by a nobleman of Padua that the *Sesamoides maius* of Dioscorides has been found in Italy, but does not say what it is. Amatus Lusitanicus was a Salamanca student, and it is just possible that he was instrumental in starting the *Reseda* theory in his University where Clusius seems to have picked it up subsequently. There was no prominent botanist at Salamanca at the time of Clusius' short visit (1565)—we know in fact that he had a very low opinion of the 'viri docti' of the Spain which he knew—and no importance can be attached to his interpretation of the two Sesamoides."

There appears to be some probability that *Sesamoides magnum* was *Ricinus communis*[*], the castor-oil plant, although Candolle identifies *Ricinus* with *Sesamoides parvum* or *album*. Sprengel states that *Sesamoides* was a kind of *Reseda*. The seeds of *Reseda*, which we have examined, are hardly comparable with sesamoid bones, but those of the castor-oil plant might well pass muster. This would suggest that the bones were called from a sesamoid plant and not from the sesame itself, did not Galen so clearly distinguish between *sesamum* and *sesamoides* and associate the bones with the former.

Both plants were largely grown in Egypt for the sake of their oils (Dioscorides, Sprengel, Lib. I, Cap. xxviii and Lib. II, Cap. cxxi), but we are informed that the root is Arabic and not Egyptian. The familiar words "Open Sesame" of the *Arabian Nights* might certainly suggest that the root SM SM was connected with a purgative. Cameron's *Arabic-English Vocabulary* gives *simsim* as sesame, millet, We have already seen that Galen associates its method of use with *panicum*. Owing to the courtesy of the Director of the Royal Gardens, Kew, we have been able to examine seeds of four kinds of millet[†], of which three might pass for reasonable comparatives, but the fourth, great millet or guinea corn, is less plausible. We cannot discover, however, that *simsim* was used in early Arabian for millet. On the contrary, Socrates Spiro (*An Arabic-English Vocabulary*, London, 1895) renders it as *coriander* seed, probably following Freytag's *Lexicon Arabico-Latinum*, Halle, 1830, who gives *simsim* = *semen coriander*.

Thus far these references might only signify a modern use of sesamum for coriander, but on consulting Lane's great *Arabic Lexicon* (p. 1420) we find that the sense of coriander is very ancient indeed. It occurs in Fairuzabadi, 1329–1414, and in Ibn Sīda's *Al-Qāmūs* of 1066. The passage from Lane cited below does not throw very much light on the matter, but indicates that either the Arabian writers copied the Greeks or the Greeks the Arabians, which alternative considering the origin of the word is, perhaps, the more likely.

["Sesame; sesamum orientale" of Linn.; applied in the present day to the plant and its grain;] "a well-known grain"; (Mṣb;) it is called in Pers. كُنْجُدْ; (MA, KL;) i.q. جُلْ جُلَانْ, (M, Ḳ,) said by AḪn to be "abundant in the Saráh (السَّرَاة), and El-Yemen," and to be "white"; (M;) [by this is evidently here meant "sesame," or the "grain thereof," or "both"; though it also signifies the "fruit of the coriander"; for otherwise, the most commonly-known meaning of سِمْسِمْ would be unmentioned in the M;] the "grain of the حَلّ"; [i.e. the "grain from which the oil called حَلّ is expressed";] (Ṣ, Ḳ; [by the author of the latter of which, this was evidently understood to be different from the جُلْ جُلَان, which is mentioned by him after the description of properties here following;]) "it is glutinous, corruptive to the stomach and the mouth; but is rendered good by honey; and when it is digested, it fattens; and the washing of the hair with the water in which it has been cooked lengthens and improves it: the wild sort thereof is known by the name of جَلَبَهْنَكْ," (Ḳ, TA,) thus, with fet-ḥ to the ج and ب and

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[*] *Sesamum silvestre*, of Pliny, which at any rate would seem to indicate that *sesamum* could be used for *sesamoides*.

[†] *Letaria italica* (Italian Millet), *Panicum miliaceum* (Indian Millet), *Pennisetum typhoideum* (African Millet), and *Sorghum vulgare* (Great Millet).

ه, and sukoon to the ل and ن, [but written in the CK جَلَبَهَنَكْ,] a Pers. word, [originally جُلْبُهَنْك,] arabicized; (TA;) "its action is nearly like that of the خَرْبَق [or "hellebore"]; and sometimes from half a drachm to a drachm is administered to him who is affected with palsy, and he is cured thereby, (Ḳ, TA,) speedily; (TA;) but a drachm thereof is dangerous, (Ḳ, TA,) in a great degree."

On the other hand the ribbed fruit of *Coriandrum sativum,* a sample of which we owe to the courtesy of the Director of the Royal Botanic Gardens, does not seem very suggestive of the sesamoid bones of the human digits*. We are thus thrown back on the following problems:

(*a*) Galen distinguishes *Sesamum* from *Sesamoides magnum,* and directly tells us that the sesamoid bones are called from the seeds of the former. But the seeds of the latter if identical with *Ricinus* are far more like sesamoid bones†.

(*b*) It is conceivable that the sesamoid bones were given their name long before Galen's day, and that like his successors he simply repeated a tag with regard to them—a commonplace of the Greek anatomists. The name being Arabic (or even possibly Persian) it is conceivable that it was applied to the sesamoid bones before it reached the Greeks.

Johannes Riolanus has a section *De sesamoideis ossiculis*‡ in which he refers to the sesamoids of hand and foot, but not to the *fabellae.* He especially notices the sesamoid bone of the great toe which he tells us the Magi called *Albadaran,* it was of the magnitude of a small pulse (*cicer*); it could not perish, and from it as from a seed the whole body would regenerate on the Day of Judgment. This tale also occurs in Cornelius Agrippa's *Liber de occulta Philosophia,* Cap. xx, with the Hebrews substituted for the Magi:

> Est in humano corpore os quoddam minimum, quod Hebraei *Luz* vocant magnitudine ciceris mundati, quod nulli corruptioni obnoxium, ne igne quidem vincitur, sed semper conservatur illaesum, ex quo veluti planta ex semine, in resurrectione mortuorum nostrum corpus animale repullulabit§.

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* Memorandum of Dr O. Stapf in reply to a letter from K. Pearson with regard to Arabic use of SM SM for coriander (Royal Botanic Gardens, Kew, 10 May 1920):

I cannot find anything in our books containing Arabic plant names that would suggest that SM SM (semsem) was ever used in Arabic for *Coriandrum sativum.* The latter is Kuzbarah in the Arabic of Egypt, Syria and India. The Greeks knew it well and the *Codex Vindobonensis* (c. 500 A.D.) of Dioscorides contains a very good figure of it. It is practically certain that the Greeks took the word sesame from the Semitic peoples of Asia, but they would hardly have mistaken it for *Coriandrum,* which has seeds (or rather fruits) of a very different appearance and taste and yields practically no fat oil. Dioscorides deals rather fully with its properties, but there is no direct allusion to a similarity with sesame, nor do his observations suggest it. Prof. Pearson may judge for himself whether there is any similarity between *Coriandrum* fruits and the sesamoid bones of man.

† While Galen uses *σησαμὶς* as equal to sesame there is some evidence that it was also used for *σησαμοειδὲς μέγα*, see Liddell and Scott's *Greek-English Lexicon* who quote Dioscorides, Noth. 4, 152.

‡ *Osteologia*, Paris, 1614, p. 483. In this work Jacob Sylvius' commentary on Galen's *De ossibus* is given and on p. 477 we read: "In pollicibus et primis digitorum articulis & in simiarum poplite sesamoidea plura, pauciora extensionem immodicam, et que luxationem minaretur, prohibentia." Sylvius (1478–1555) antedates Vesalius (b. 1514); he clearly knew of the *fabellae* in apes, and may well have started Vesalius on the discovery of those in man.

§ See also Hyrtl, *Das Arabische und Hebräische in der Anatomie,* S. 165 *et seq.* Further Joannis Munnics, *De re anatomica*, Treves, 1697, p. 213.

Thus the seedlike character of the sesamoid bone is preserved in both the Arabian *Albadaran* and the Hebrew *Luz* with their mythical associations*. It would be of great interest to know the age of these myths. If the Semites before our epoch had discovered the sesamoid bones and attached these legends to them, there might be no weight at all in Galen's explanation of sesamoid as like to the sesame-seed—the whole idea and terminology may be Semite and not Greek, and Galen may have become acquainted with it in Asia Minor.

(3) *History of the Sesamoids of the Knee-Joint. First Period—that of isolated Records of Anatomical Writers.*

From the Greeks down through the Middle Ages the study of anatomy was essentially the study of human anatomy; references to dogs or apes are few and far between and then very superficial in their associations†. Probably Jacob Sylvius' reference to the *fabellae* in apes is the first note we have of the existence of sesamoids of the knee-joint (see our footnote ‡, p. 12). There is no evidence that the Greeks or Arabs were acquainted with them. Vesalius was the first to draw attention to their existence in man. In his *De corporis humani fabrica*, Lib. I, Cap. xxviii (Basel edition, 1555, p. 153, Leyden edition, 1725, Tom. I, p. 107) he writes:

> Deinde bina recensebit in poplite occurrentia ossicula, quae duorum primorum pedem moventium musculorum innascuntur capitibus, mox in illorum ex femoris osse principio. Ossicula enim haec laevi sua et lubrica superficie, qua extra musculorum substantiam prominent, elatiorum spectant sedem posterioris regionis inferiorum femoris capitum, quorum impetum illa solvunt & sustinent, hoc privatim sibi vindicantia, quod musculorum exortibus, non vero aliorum fere omnium ossiculorum sesamo comparatorum modo tendinibus innectantur.

It is curious that in this passage Vesalius speaks as though the *fabellae* were constant in man, and this although as we shall see the mesial *fabella* is very rare indeed, and the lateral *fabella* does not exist in more than seven to ten per cent. of cadavers. It is further noteworthy that he does not state that he has definitely in a given cadaver discovered sesamoids in the heads of *M. gastrocnemius.* He speaks as he might have spoken of the sesamoid of the great toe with fifteen centuries of history behind it. There is no statement of a new discovery, nor that the occurrence is not universal. He writes as he might write of the patella itself! We have not succeeded in finding any reference to the *fabellae* in Vesalius' work of 1543*.

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* The word *Luz* signifies a tree producing a small nut or the nut itself. In Genesis xxx. 37 it occurs and is rendered in the English version by "almond." Rashi, prince of commentators, explains it as chestnut, but it has been interpreted of any tree bearing small nuts, or almonds. Its secondary meaning in Rabbinic literature is a bone or cartilage resembling the almond said to be in the vertebral column of man. It was quite possibly the word used by Jewish anatomists for the sesamoids.

Commenting on the words "And the almond tree shall blossom" we read in the *Midrash* (Ecclesiastes xii. 5: see also Genesis, Ralba § 28, and Leviticus, Ralba § 18) the following:

R. Levi says, This is the "Luz" (i.e. almond-shaped bone) of the spinal column. Hadrian once asked R. Joshua b. Hananiah from which part of the body of man shall he blossom forth in the life of the future? And he answered "From the 'Luz' of the spinal column." He then said: How so? They then brought such a "Luz," put it in water, and it did not dissolve finally; into fire, and it was not burnt; into the mill, and it was not ground; they put it on a block and beat upon it with a hammer, and the block was split and the hammer broke, and all was of no avail [to destroy it].

The *Midrash Ralba* is a very old collection of Hebrew lore, parts of which are probably antecedent to the Talmud recension. We have to thank our colleague Dr Hermann Gollancz for the above references. We think it probable, however, that Jewish anatomy was non-existent before the appearance of the Greek followed by the Arabian medical schools.

† The first *Simiae Osteologia* is due to the elder Riolanus and edited by the younger in the *Osteologia*, Paris, 1614. Caput xxvi is entitled: *De sesamoideis* and we read (p. 535), "Duo ossicula magnitudine ciceris supra utrumque tuberculum femoris in origine gemellorum reperiuntur."

The next reference we have been able to find to the *fabellae* occurs in Eustachius' *Opuscula Anatomica* issued in 1564, but the permission to print which dates from 1562. We have quoted the relevant passage in the footnote to our p. 6. We seem on reading Eustachius' words to be in the atmosphere of a man who had really examined the matter in many cases, and we are almost inclined to wonder whether, if Eustachius had been able to get his works printed when they were written†, Vesalius would have been the reputed discoverer of the *fabellae.* At any rate Eustachius' statements are correct, and here as elsewhere he not only criticises Vesalius, but does so legitimately‡.

Fallopius in his *Observationes Anatomicae* of 1561 (fol. 113) says that the *fabellae* are frequent in apes and that he has seen them, but that only Vesalius has seen them in man.

At the end of the 16th and beginning of the 17th centuries we have Caspar Bauhin. He has in his works a good deal about sesamoid bones. In his *De corporis humani fabrica* (Basel, 1590) there are references to the sesamoids on pp. 356, 372, 395, but we have failed to examine a copy, and cannot say whether he refers to the *fabellae*, but he probably does. In his *Anatome* (Basel, 1597), after enumerating (p. 259) *sesamina duodecim* of hand and foot, he continues "Hic addere possimus sesamina duo in poplite§." Again in his *Theatrum Anatomicum* (Frankfurt, 1603) he has considerable references to sesamoid bones (pp. 1169—1171, 1207, 1277—80), and for the *fabellae* (p. 1278). He gives, Tab. XV, Fig. 11, diagrams of the sesamoid bones of the hand and foot, even the very small ones, but not of the *fabellae.* This leads us to believe that he had never seen the latter. Confirmation for this view arises from the fact that what he says is principally paste-and-scissors-work from Galen and Vesalius. Speaking generally of sesamoids in his Cap. XXIX, he does say, however, "solida sunt, rotunda, aliquantulum depressa, aliquando cartilaginosa, aliquando ossea." This may be original, but is most probably due to an earlier writer in a passage which has escaped us.

Lastly in Bauhin's *Institutiones anatomicae*, Basel, 1609, he refers to sesamoids in each head of origin of *M. gastrocnemius* (p. 247).

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* The first edition of his anatomy which appeared at Basle in this year.

† As to Eustachius' difficulties in publication see *Biographie Universelle*, Paris, 1815, Tom XIII, p. 534.

‡ Eustachius' writings seem to indicate some deep ground for dislike of Vesalius. Can it be that unpublished discoveries of Eustachius were talked about and made use of by Vesalius in his great work? At any rate Eustachius clearly knew more about the *fabellae* in man than Vesalius did.

§ This statement of the *fabellae* being *in poplite* must not be taken as referring to the popliteal muscle's origin, but simply when met with in the early anatomists as indicating the neighbourhood of the popliteal surface.

It will be clear that Bauhin does little more than confirm the error of Vesalius by speaking as if the *fabellae* were constant in man and occurred equally in both heads of origin of *M. gastrocnemius.* To this nearly universal overlooking of Eustachius, and to the parrot repetition of the views of Vesalius we owe most of the obscurity about the *fabellae* which followed their discovery. In Riolanus, the Elder, *Osteologia*, Paris, 1614 (pp. 69, 121, 123, etc. of the *Isagogica de ossibus Tractatio*), we have not been able to find references to the *fabellae*. There is only the passage already cited (see our p. 12, footnote ‡) with regard to the "in simiarum poplite sesamoidea" in Sylvius' commentary on Galen's *De ossibus* (p. 475) and the reference to the *fabellae* in the apes in the *Simiae Osteologia*, p. 535. The younger Riolanus in his *Anthropographia*, Liber v, Paris, 1650, Cap. xliii, p. 333, writes:

> Externus gastrocnimius (sic!) ab externo condylo nascitur...singulis eorum principiis primus Vesalius observavit singula ossiculis sesamena apposita, saepius alterum deficit, authore Fallopio. Ut laevi lubricaque sua superficie, dum ossi & musculo interjecta sunt, impediant ne in cruris directione musculi atterantur aut ab osse laedantur.

The direct attribution to Vesalius is here made and Fallopius is cited, not Eustachius, as casting some doubt on the constant appearance of at least *one* of the *fabellae.*

Gorraeus in 1601, Paaw, 1615, and Laurentius in the same year (also in 1628) confine their attention to the sesamoids of hand and foot*.

In 1632 we find published at Frankfurt Adrian Spiegel's *De humani corporis fabrica*, and on p. 78 under *Gastrocnemius externus* we read:

> Huius musculi duobus capitibus, quemadmodum Vesalius notat non procul ab exortu sesamoidea ossicula tributa sunt.

In the *Tabulae anatomicae* of J. Casserius, edited by D. Bucretius (Frankfurt, 1632), which accompany Spiegel's work, Tabella XXXVIII, Fig. 11, professes to give a diagram of *gastrocnemius.* The figure represents the lower limb from knee downwards, the muscle appears to be cut at the two points of insertion and turned back from the knee, and S, S, two sesamoids, in it appear to rest on the ground. The figure is somewhat obscure, but it is the first professed representation of the *fabellae*, probably largely a product of the imagination (see our Plate I, Fig. 1). Dominicus de Marchetti returns to the healthy statement of his own personal experience. He rightly holds that, while he himself has not found the *fabellae* in the many bodies he has dissected, he cannot deny their existence. But that they are certainly not found in all bodies as Vesalius and Riolanus have asserted†.

Thomas Bartolinus in his *Anatomia reformata*, Hagae Com., 1655, returns very nearly to the Vesalius legend. In Liber IV, Cap. xxii, *De ossibus sesamoideis*, p. 528, we read:

> Item bina ossicula in poplite juxta os femoris, musculorum (duorum priorum pedum moventium) non tendinibus, sed principiis uniata, quae in senibus reperiunter, & animalibus siccis, ut cervis, canibus et leporibus.

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* There is also no reference that we have been able to discover in the Sylvius of 1635.

† *Compendium anatomicum*, Patavii, 1652, p. 167, and *Anatomia*, Padua, 1652, p. 153.

How these mediaeval anatomists used each others' very words! There is, however, the qualifying phrase soon to become a part of the myth, that the *fabellae* occur in the aged. Further the deer and the hare are added to the list, man, ape and dog, that own *fabellae*. This reference to the aged is emphasised again in the edition printed at Leyden, 1686, p. 756.

Diemerbroeck, *Anatome corporis humani*, Utrecht, 1672, p. 944, is content to return to the complete Vesalius legend, and finds two *fabellae* and these always occurring. Stephen Blancard's *Anatomia reformata*, Leyden, 1695, p. 729, and Gerhardus Blasius' *Anatome hominis*, Amsterdam, 1673, p. 62, give also the complete Vesalian story. But the 17th century is not to close without one or two cases of men who report what they have actually seen. Thus Schrader in 1674 reports that he had found a *fabella* in the anatomy of a *cadaver virile**, and that sturdy old surgeon-anatomist William Cowper, in his *Myotomia reformata*, London, 1694, p. 206, states first the opinion of Vesalius and Riolanus:

> that in the two beginnings of this muscle there are two *Ossicula Sesamoidea*, which we must acknowledge with Marchetti have hitherto escaped our Observation though it is likely it may be so in Aged Bodies, as it appeared in a subject I lately dissected on one side only.

We might almost say that from the reported discovery of Vesalius, only Eustachius, Schrader and Cowper had really seen a *fabella* up to the end of the 16th century.

Even in the case of Cowper we are to find later that the dogmas as to the appearance of *fabellae* in the aged, and as to their object, are accepted. Thus in his *The Anatomy of Human Bodies*, 2nd edition, Leyden, 1737, T. 103, F. 2, under *Ossa sesamoidea*, we read:

> In some Bodies especially Aged, we find Two Ossa Sesamoidea on the Superior Parts of the Two Lower Heads of the Thighbone D, E: The Office of which is to Defend the Bending Tendons of the Tibia from too great a Collision on those Heads of the Bone which they would else be subject to.

At the very end of the century Joannis Munnics, in his *De re anatomica*, Treves, 1697, p. 213, sums up the pure Vesalian doctrine:

> In censu quoque ossiculorum sesamoidum poni debent duo, quae in poplite inferioribus femoris appendicibus apponuntur, duorum priorum pedem moventium musculorum principiis inhaerent.

For him all sesamoids also start as cartilaginous and become solid with the progress of age.

Thus far the history of the *fabellae* has been fully representative of an oft-occurring scientific tragedy. Authority dominates inquiry and dogma fills up the space with its story of how a non-existing phenomenon (the constant appearance of both *fabellae* in man) arises and what purpose it serves. The time was therefore ripe for a little comedy, and very early in the 18th century we find this in a double fashion, the Trew-Heister incident. In 1715 C. J. Trew wrote an Altorf Dissertation entitled *De chylosi foetus in utero*. Tabella II contains a large but crude drawing of a lateral *fabella* resting in a cavity on the condyle. There is a separate drawing of the sesamoid itself (FVI) (see our Plate II, Fig. 4). Trew's thesis was republished by Haller, *Disputationum anatomicarum selectarum*, Volumen v, Göttingen, 1750, p. 475. Figs. v and vi should give the *fabella*, but the plate is missing in the two copies of Haller that we have examined, possibly the plate never existed in Haller. The description to Fig. v, C is "C est os sesamoideum insidens cavitati condyli exterioris in omnibus femoribus conspicuae." This sesamoid (if only a lateral *fabella*), and the cavity conspicuous in all femora, were something extraordinary, and Trew seems to have thought so, for he writes as follows:

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* *Observationes anatomico-medicae*, Amsterdam, 1674, p. 193.

> *Observatio II. Ossicula sesamoidea in femore ac minimo manus digito.*
>
> Cum aliquando occupatus eram in ossibus humanis a carne sordibusque mundandis, atque accurate in praeparatione artuum in numerum ossiculorum inquisiverim, cum primis deprehendi numerum sesamoideorum auctum. Primum mihi antea nondum cognitum se offerebat in femoris parte inferiori, ubi cum tibia articulatur, in condylo exteriori: ubi in fovea quadam deprehendi ossiculum rotundum figura & magnitudine Fig. VI. quod instar parvae patellae loco C. Fig. V. insidebat in utroque femore. Putabam tunc temporis, id extraordinarium fuisse; dum vero illud postmodum inquisivi in aliis femoribus, luculenter semper deprehendi foveam in loco, cui insidet, ita ut deinceps ulterius illius existentiam perscrutari excitarer; quod & mihi nunquam non in tot, quotquot deinceps cadavera inspicere poteram, reperire contigit; siquidem brevi in quatuor illud inveni, atque etiam forsan cuilibet inquirenti patebit.

It will be observed that Trew does not say that he has ever discovered a mesial *fabella*. But such a big discovery was too much for Trew's anatomical instructor, Lawrence Heister. In the first edition of his *Compendium anatomicum*, Nürnberg, 1719, he magnified Trew's lateral *fabella* into two *fabellae*, he forgot to mention Trew's name and he proclaimed the discovery of two new bones! One might at least have supposed an acquaintance with the text-books of his day. The English translation of Heister's work, *The Compendium of Anatomy*, London, 1752, appears to have been made from the earliest edition of Heister, and does not contain the long apologetic note of the Nürnberg edition of 1732 (Vol. II, p. 47) or the Amsterdam edition of 1748 (Vol. II, p. 48). We read on p. 65:

> There remain now to be considered, the *ossa sesamoidea*. These are small bones, and are most conspicuous in old subjects; they somewhat resemble the seeds of the sesamum, whence they have their name. Their most usual situation is...[details of sesamoids of hand and foot] one frequently in each external condyle of the *os femoris* (Tab. I. figs. 2, 3, 4)...... These are usually found in adults, or in elderly people: sometimes though more rarely there is one also in the internal condyle of the *os femoris*...... Upon the whole there are very rarely found more than sixteen of them often fewer. Those anatomists, therefore err greatly who reckon more than forty of them......too many, however, have given in to this error.
>
> All these bones, except those that are found in the condyles of the femur, adhere to the tendons of the muscles: those excepted, are connected to the origin of the muscles. Their size and shape are various and irregular: they are cartilaginous in young subjects, but they grow hard and boney by age: and it is therefore that they are so much the more easily found in old people. They serve as a kind of trochleae to the muscles and increase their power.

On p. 463 Heister gives an "Explanation of the Figures" (see our Plate II, Fig. 5):

> Fig. 2. Represents the lower part of the *os femoris* with two sesamoid bones not described by other authors. A, The *os femoris*. B, The internal condyle. C, The external condyle. D, The larger of the two new sesamoide bones, situated in a considerable cavity in the external condyle. This, however, in some subjects, is much larger than it is represented here. E, The lesser of the

two new sesamoide bones, situated in the internal condyle. This is but very seldom met with in dissection, most subjects wanting it: but the other is seldom wanting.

Fig. 3. Represents the larger of these two sesamoide bones, separated from the cavity in the external condyle, in which it is generally lodged.

Fig. 4. Shews the lesser sesamoide bone, of the internal condyle, separate.

Apparently Heister was not left long to enjoy his triumph at the discovery of "two new sesamoide bones." In the long and somewhat abject note of 1732, he admits that the "rediscovery" was due to Trew; he cites a few authors of the past who did not refer to the *fabellae*, but he does not adequately explain why he had apparently overlooked Vesalius, Eustachius, Riolanus, Cowper, etc. Indeed "rediscovery" is hardly the right description for the *fabellae* in 1715, when W. Cheselden* could write in *The Anatomy of the Human Body*, 1713, pp. 22—23:

> *Ossa Sesamoidea*...and sometimes one in the lower end of each Thigh-bone at the beginning of the *Plantaris* muscle. Their use is the same with the Patella.

A brief and pregnant sentence almost the most suggestive since that of Eustachius. Another remarkable point is that Heister should have "rediscovered" the suppositious influence of old age, one of the points the 17th century writers had much emphasised.

Gruber† throws complete discredit on Heister's statements and especially on his plate. He says that Heister has placed the *fabellae* where they do not usually exist, and apparently Gruber considers that if they occurred at all they must have been pathological osteomata. Yet Heister says that he has found them in four corpses, one after another, and that they can always be found except in youthful cadavers, where they are cartilaginous‡! We are by no means certain that Heister's drawing, as far as the lateral *fabella* is concerned, is not a rough copy of the crude diagram in Trew's Dissertation of 1715; both exhibit the lateral *fabella* resting in a hollow, not of the articular surface, but of the lateral condylar eminence in its proximal part. As for the mesial *fabella*, which Trew does not provide, Heister rests it, the femur being vertical, on the commencement of the popliteal area as it springs from the articular surface of the mesial condyle: see our Plate II, Fig. 5. We believe the whole drawing to be imaginary copied from no actual subject, and totally out of accordance with all skiagrams of the lateral *fabella* in man with which we are acquainted. Not one of the first three drawings, Casserius (1632), Trew (1715) and Heister (1717), appears to us to represent in any way the *fabella* as it exists in man. The comedy of Heister on the *fabella* might well be preserved in the history of science as an illustration of the process of concocting a text-book.

Saltzmann§ (*Decas observationum illustrium anatomicarum*, p. 6), Strassburg, 1725, reports that he found no *fabellae* on the condyles of a given cadaver. Bass (*Observationes anat.-chirurg.-med.*, p. 220), Halle, 1731, and Albinus (*Historia*

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* He did not apparently return to the subject in his *Osteographia or the Anatomy of Bones*, London, 1733.

† Gruber, p. 11, footnote.

‡ *Academiae Cassareo-Leopoldinae Naturae Curiosorum Ephemerides Centuria* VI. Obs. XXIX. pp. 245—6, Ossa sesamoidea in femore...Francofurti et Lipsiae, 1717. See also *Centuria* VII. Obs. XXIII. pp. 49—51, 1719.

§ For fuller details of the following eight references; see Pfitzner's bibliography.

musculorum hominis and other works), 1734—1757, have no reference to the *fabellae*. Palfin (*Anatomie chirurgicale...du corps humain*, Vol. II, p. 159), 1726—1734, says they are not always to be found as Vesalius believed, while Winslow (*An Anatomical Exposition of the Structure of the Human Body*, London, 1749, and *Exposition anatomique de la structure du corps humain*, Paris, 1732) apparently considers they are always to be found, and in cartilage-lined hollows. George Thomson (*Anatomy of Human Bones*, London, 1734, p. 104) asserted the existence of both, which was the view taken by Kulmus in his *Tabulae anatomiae* (p. 62) of 1732 and supported by the authority of Haller in 1745. In such a sea of wearisome positive and negative assertions unaccompanied by personal examination, it is almost a comfort to meet such a bare statement as that of Drake in his *Anthropologia nova*, 3rd edition, 1750, p. 434:

> There are sometimes found two *ossa sesamoidea* in the two beginnings of the *Gastrocnemius externus* muscle, but they are rarely met with and only in aged Bodies.

He at least knew that they did not always occur or fail to occur, even if he supposed no difference in frequency of the pair. Still more comforting is Morgagni's statement (*Adversaria anatomica*, T. II, Leyden, 1723, p. 64*) that he had found the lateral *fabella* several times, but the mesial *fabella* only once. It goes at any rate a little way to balance the statements of Lieutaud (1742) that he had found *fabellae*, more often mesial than lateral, of Disdier (1745) that one usually exists in the groove behind the lateral condyle, of Lauth (1798) that he had never found any *fabellae*, and of Bertin (1783) that he had found two on each femur!

How strikingly barren these 18th century anatomists seem to have been, at least in this matter of the knee-joint! It is not till the very end of the century that with Sömmering and Peter Camper we get some progress in our problem, and we begin again to grasp the difference between big and little naturalists. We will take the former first because his contribution is less important than those of Camper.

Sömmering (*Vom Bau des menschlichen Körpers*, Leipzig, 1791, Bd. III, S. 295) recognised that a *fabella* is not infrequent in the lateral head of *M. gastrocnemius*. He continued to study the subject, however, and in his *Lehre von den Muskeln* of 1841, S. 347—351, he recognised that the lateral *fabella* is often only a hemisesamoid, i.e. cartilaginous, and that the mesial *fabella* is very rare, and when it does occur is far more likely to be a hemisesamoid than an orthosesamoid. Further like Cheselden (see our p. 18) he recognises a relation of the lateral *fabella* to *M. plantaris*:

> Der Ursprung des *M. plantaris* hängt mit der Ursprungsehne des lateralen *Gastrocnemius*-Kopfes, namentlich auch mit dessen Sehnenbeinchen eng zusammen.

We are clearly in touch with a man, who is observing and thinking on his own.

Peter Camper's first contribution occurs in his *Dissertatio de fractura patellae et olecrani*, Haag, 1789, translated as *Abhandlung von Bruch der Kniescheibe und*

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* His words are: "Nos certe quod alterum eorum in nonnullis cadaveribus et in uno internum nominatim invenisse meminimus." They do not occur in the edition of 1714 but will be found in the Venice edition of 1782.

des Olecranon, reprinted in the German translation in the *Vermischte Schriften*, Lengen, 1801, S. 68, and Plate I, Fig. i. K. We read (see our Plate III, Fig. 6):

> A, K, I, L die Sehne des äusseren Bauchs des Wadenmuskels (*Gemelli seu gastrocnemii externi*) worin sich ein Knöchelgen (*ossiculum sesamoideum*) f. g. findet welches man in den inneren Bauch derselben nie sieht. Es wird bei den Affen, den Orang ausgenommen, bei dem Hunde allzeit in beiden Portionen, auch beim Fuchse, bei der Katze, dem Igel, in dem Agu und allen Thieren gefunden.

The statements are too sweeping, but they are those of a man who is stating what he knows of his own observation, and are not the mere reiterations of his predecessors. We are beginning also to get a wider range of comparative observation—comparative anatomy is starting its career.

We have reproduced a sketch of Camper's diagram of the "Knöchelgen" near K on Plate III, it is far from an ideal representation, but it is a great advance on those of Casserius, Trew and Heister. We next turn to Camper's *Naturgeschichte des Orang-utangs*, Düsseldorf, 1791, S. 126, and note that Camper, after citing Eustachius' view about Galen and the *fabellae* in man, continues:

> Hier muss ich aber Eustach aus eigener Erfahrung widersprechen, weil ich dieselben in sehr vielen Körpern sowohl von Männern, als Weibern, doch allein in äussern Kopfe des Wadenmuskels oder Gastrocnemius, gefunden habe. In meiner Sammlung habe ich eine grosse Menge derselben aufbewahrt. Am meisten wundere ich mich, dass Albin derselben gar nicht erwähnt, da Eustach sehr deutlich sagt, dass er diese Beinchen nicht selten bei Menschen, in Affen und Hunden aber immer gefunden habe. Nicht allein Eustach hat dieses wahrgenommen, sondern auch Coiter (59) und Sylvius dem Blasius (60) zufolge, kannten den Sitz derselben in den Affen sehr wohl, dass sie nämlich in beiden Köpfen der Gastrocnemii in den Affen, bisweilen in der Sehne des Peroneus Longus und Tibialis zu finden sein: dieses kann ich in verschiedenen Affengerippen, und selbst ein Sesambeinchen in der Tibialis eines weiblichen Gerippes zeigen.
>
> Im Orang, auch im Rumpfe des Orangs, der im Thiergarten des Prinzen von Oranien gelebt hat, habe ich keine gefunden—ich bin auch gewiss, dass sie nicht da waren, weil ich sonst den Knorpel müsste angetroffen haben, so wie ich das deutlich in der Sehne des Muskels Popliteus fand, und noch aufbewahre. Tyson spricht auch nicht davon, und bei dem allen findet man sie immer in den geschwänzten Affen, im Pithecus oder Aegyptischen Affen, in den Hunden, Katzen, Füchsen, Stachelschweinen und dergleichen, und zwar doppelt.

Further on S. 187 we read:

> Von dem Knie werden wir nichts mehr sagen, als dass ich in der Sehne Kniescheibenmuskels (popliteus) ein sehr grosses, doch knorplichtes Sesambeinchen gefunden habe. Nicht allein im Rumpfe, sondern auch in dem Orang des Hoffmann, das ist, in meinem ersten traf ich ein solches Bein an.
>
> Dieses Sesambeinchen konnte meiner Aufmerksamkeit destoweniger entwischen, weil es nie beim Menschen, sondern immer in den Pavianen, Hunden, Fuchsen, Katzen u. s. w. angetroffen wird.
>
> Ich sahe also gleich das Werk des Tyson nach, weil Cowper, der sich durch die Zergliederung der Muskeln so berühmt gemacht hat, auch die des Pigmy beschrieben hatte.—Doch anstatt hier einiges Licht anzutreffen, fand ich diese offenherzige Erklärung, dass ihm dieser Muskel entgangen sei (70). Auch suchte ich vergebens in der uns vom Daubenton mitgetheilten Zergliederung des Gibbon nach demselben.

According to Peter Camper we have accordingly:

(*a*) Both *fabellae*, the lateral and mesial, in a variety of apes, in dogs, cats, hedgehogs, etc.

(*b*) In man only a single *fabella* occasionally, and this on the lateral condyle.

(*c*) A sesamoid in the tendon of the popliteus (which we term the *cyamella lateralis*) in the orang, but no *fabellae*.

(*d*) No *cyamella lateralis* in man, but it does occur in baboons, dogs, foxes, cats, etc.

Most of the above statements of Camper's can be confirmed, but there are certain exceptions, notably the *cyamella lateralis*, the sesamoid of the popliteal tendon, has been found in man, but it is very rare. Thus while it required 14 centuries after Galen to establish the existence of the first two sesamoids of the knee-joint, the *fabellae*, in man and nearly 250 years after Vesalius to reach the third sesamoid, the *cyamella lateralis*, in the orang, it took 80 years after Camper to establish the *cyamella* as an occasional anomaly in man. Such is the slow growth of scientific knowledge as evidenced in a single anatomical detail like the present. It must not, however, be supposed that with this rapid increase of knowledge in the last years of the 18th century, the 19th century would see rapid progress in our anatomical knowledge of the knee-joint. On the contrary the inertia and follow-the-other-fellow policy of the first half of the 18th century reappears in the 19th.

Cloquet in 1816 (*Traité d'anatomie descriptive*, Paris, I, p. 205) assures us that the *fabellae* appear fairly persistently on both condyles of the femur in man. Bourgery (*Traité complet de l'anatomie*, Paris, 1831, II, p. 103) after describing the *M. gastrocnemius* continues:

> Parfois chez les vieillards des os sésamoïdes se développent dans leurs tendons fémoraux, surtout dans celui du jumeau interne (!).

Indeed no treatise of anatomy could be complete without these "vieillards"; we have followed them through the centuries. The doubting Thomas, however, is always with us. Sappey as late as 1876 (*Traité d'anatomie descriptive*, Paris, II, p. 430) denies the very existence of *fabellae* in man! Even the modern English text-books of anatomy often do not exhibit a knowledge of the sesamoid of the knee-joint comparable with that of Eustachius, or as suggestive as the remark in Humphry (*A Treatise on the Human Skeleton*, 1858, p. 537):

> Where this band (posterior ligament of the knee-joint = *lig. popliteum auct. ab semi-membranoso*) joins the *gastrocnemius* upon the outer condyle of the femur is commonly a thick mass of fibrous tissue and sometimes a sesamoide bone (Pl. 51, Fig. 2D*) is developed.

Humphry (see our Plate IV, Fig. 7) is clearly adding to the accumulating knowledge of the mass of muscular attachments associated with the lateral *fabella*;

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* This is we think the *fifth* representation of a *fabella*. Gruber (Gruber, p. 7) suggests that Weitbrecht (*Syndesmologia*, 1742, Fig. 57, *h*) shows a *fabella*: "hat es vom Ursprunge bedeutend entferut (etwas 2 cent.) im *Gastrocnemius externus* abgebildet, aber un Texte nicht bezeichnet." Pfitzner (Bibl. Pfitzner, S. 758) denies this. It is possible that Weitbrecht or his artist indicated something they did not understand, but the plate is too obscure to allow us to come to any conclusion whatever, and as Weitbrecht does not refer to the point in his text, the matter is not of the slightest real importance. There could not be another rediscovery of the *fabella* in 1742!

we have already cited in this direction Cheselden and Sömmering (see our pp. 18 and 19). Quain, however, in 1867 (*Elements of Anatomy*, 7th edition, London, Vol. I, p. 284) can tell us nothing more than:

> A sesamoid fibro-cartilage is sometimes met with over the outer condyle and occasionally over the inner, it is rarely ossified—

a statement which is apparently incorrect in at least two points;—while Gray as late as 1905 (*Anatomy, Descriptive and Surgical*) is content with the assertion that there is a sesamoid fibro-cartilage (rarely) osseus in the tendon of the outer head and one occasionally in the tendon of the inner head—another statement too brief to be in any way accurate.

The German anatomists have been somewhat more precise. Hyrtl in 1838 ("Physiologische anatomische Bemerkungen über die Kniegelenksknorpel," *Medicinisches Jahrbuch d. K. K. Oesterr. States.* Bd. XX, Wien, S. 31—32) tells us that the *fabella lateralis* is more frequent than the *fabella mesialis*, that they may be hemisesamoids, and that he has found them in both heads of *M. gastrocnemius.* Again in his *Lehrbuch der Anatomie der Menschen*, 12 Aufl., Wien, 1873, S. 420, after stating that Camper had only seen *fabellae* in the external head, he continues: "Nach meinen Beobachtungen kommt es in beiden Köpfen vor, obwohl in äusseren ungleich häufiger." Lastly we may note that Gegenbauer in 1890 (*Lehrbuch der Anatomie der Menschen*, Leipzig, S. 457) has for a text-book a fairly complete and adequate statement.

Before we come to the important memoirs of the last quarter of the 19th century which have made the sesamoids a special study we ought to note an important memoir by Macalister of 1872 (*Muscular Anomalies in Human Anatomy*, Dublin, 1872*). It is important for our purposes for three reasons:

(*a*) Because it provides evidence for the existence of the mesial *fabella* in man:

> Gastrocnemius—1. May have a sesamoid bone in its inner head: I have found it: 2. Or in its outer—this is more common. (p. 118.)

Macalister clearly speaks here of an orthosesamoid, not a hemisesamoid.

(*b*) Because it gives the first statement of the existence of the *cyamella lateralis* as an anomaly in man.

(*c*) Because it records anomalies of the popliteus muscle which have considerable bearing on both the *fabella lateralis* and the *cyamella lateralis.*

> Popliteus muscle has been described as double (Fabricus ab Aquapendente: "De Motu locali Animalium" in *Opera Anatomica et Physiologica*, Lipsiae, 1687, p. 359). The same has been seen by Professor Bevan, of the Royal College of Surgeons, Ireland....A small superior popliteus, arising from the outer condyle, and above the popliteus muscle, to which it was united, and inserted into the upper part of the tibia, was seen by Calori†. A sesamoid bone has been found in its tendon. Slips from the semi-membranosus have been found inserted into the fascia over this muscle.

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* Also as *Transactions Royal Irish Academy*, Vol. XXV 1872. J. F. Knott, "Muscular Anomalies," *Proc. R. Irish Academy*, Second Series, Vol. III, p. 639, 1882, notes a case of bilateral orthosesamoid in tendon of *Popliteus.*

† *Mem. della Accad. delle Scienze dell' Istituto di Bologna*, 2 series, Vol. VI, p. 143, refers only to the supernumerary popliteal muscle not to sesamoids.

The bearing of the whole of this paragraph on Gruber's later work is important, and it is regrettable that he did not give more consideration to its statements.

The exact position of affairs with regard to the sesamoids of the knee-joint in man in 1872 was as follows:

(i) The erroneous statement of Vesalius, at once corrected by Eustachius, had been more or less discarded, even in the text-books.

(ii) The existence of the lateral *fabella* in man was recognised as a not uncommon occurrence and it might be an orthosesamoid or a hemisesamoid. If the latter it was described as "fibro-cartilaginous."

(iii) The existence of the mesial *fabella* was realised to be something much rarer, and less often an orthosesamoid. It was, however, vouched for by such credible observers as Eustachius, Morgagni, Sömmering, Hyrtl and Macalister, and by the less credible Heister.

(iv) There was a growing realisation that in man the *fabella lateralis* had relationship not only to the tendon of the outer head of *gastrocnemius*, but to *M. plantaris* (Cheselden and Sömmering) and to the posterior ligament of the knee-joint (Humphry).

(v) Camper had discovered the *cyamella lateralis* in the orang as a persistent feature, although the *fabellae* are absent. He had found it accompanied by the *fabella lateralis* in certain of the lesser apes, and such association is invariable in the cat*. There was really no excuse in 1872 for confusing the lateral *cyamella* with the lateral *fabella*. While Camper denied the existence of the *cyamella* in man, Macalister had discovered it as a rare anomaly.

(4) *History of the Sesamoids of the Knee-Joint. Second Period—that of Monographic Literature.*

The three chief memoirs to be now considered are those of Gillette (1872), Gruber (1875) and Pfitzner (1892). Of these authors Gillette and Pfitzner consider all the sesamoids of the human skeleton, Gruber only those of the knee-joint, and of these he realises only the *fabellae*.

(*a*) Gillette's paper is entitled "Des os sesamoides chez l'homme," *Journal de l'Anatomie et de la Physiologie*, pp. 506—538, Plate XX, Paris, 1872. Gillette commences by dividing sesamoids into *peri-articulaires* and *intra-tendineux*—this distinction is not without its uses. He says, however, that the first are true bones and the second are not (p. 535). He admits, however, when he comes to the *fabellae*, which clearly are intratendinous, that they, apparently because they are more voluminous, have greater resemblance to the periarticular sesamoids. He gives in his Fig. 16 the first really good illustration of the *fabella lateralis in situ*. We have reproduced it in our Plate I, Fig. 3.

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* See *Mammalian Anatomy* of Horace Jayne, London and Philadelphia 1898. Part I. The Skeleton of the Cat, pp. 704—5.

Gillette (p. 533) asserts that in the foetus and the child there are no traces of the *fabellae*. This is, of course, opposed to Nesbit's conclusion, but as in perhaps nine cases out of ten no trace of the *fabellae* can be found in the adult, his assertion is like Gruber's by no means conclusive*. Gillette is a strong supporter of the intensive stress theory of the origin of sesamoids. He asserts that little by little:

> par le frottement le tendon s'élargit, s'aplatit, devient plus dense. Il se produit à ce niveau et dans son épaisseur un épaissement d'abord fibro-cartilagineux, c'est *l'os sesamoide intra-tendineux cartilagineux*, mais sous certaines influences toujours de nature mécanique, il se dépose des molecules osseuses dans l'intérieur de ce noyau qui se constitue *os sesamoide osseux* (p. 534).

The argument seems to us of precisely the same character as the argument that the environment produces the plant. In a certain sense it does, but the seed contains the potentiality of the plant. We might argue that nourishment and exercise produce the human skeleton, and it is only in this sense, that the *fabella* is no more the product of mechanical causes than the femur itself, that we can accept Gillette's statement. We believe, however, that both he and other supporters of the theory of intensive stress mean a great deal more by it than we are willing to admit. Some decision might be made by the examination of the puppy in various stages of growth, we should be much surprised, if the intense activity and restlessness of a young puppy could be subdued, to find it growing up without or even with much diminished *fabellae*!

The classification of sesamoids into intratendinous and periarticular is convenient, but to identify these with hemisesamoids and orthosesamoids seems to us extremely doubtful, and to state that the former pass into the latter owing to mechanical causes we do not find at all helpful.

(*b*) *Gruber's Monograph*†: This memoir exhibits all the surpassing merits and some of the small but disturbing faults of this eminent anatomist. It presents Gruber's usual wealth of new material and his extensive knowledge of earlier literature. We have at once a sweeping clearance out of all the old anatomical myths, and the forcible statement of new and sounder ideas based on wider ranges of observation. For the first time in the history of our subject we have adequate material directly examined and recorded. Again for the first time we have a real attempt made to record the appearance or non-appearance of the *fabellae* in various living forms. We begin to realise at once that as in the case of man, so in the case of many other living animals the contradictions of earlier writers chiefly arise from want of adequate material; the problem is not whether *fabellae* do or do not exist, but in what proportion of cases they will be found. In other words it is not the "always-present" nor "always-absent" categories that are the difficult ones, but the "sometimes present" category—needing statistical treatment—which is the hardest to ascertain and yet is, perhaps, the most valuable for evolutionary suggestion.

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* It is needful to take a case where a *fabella* always occurs, e.g. the dog, and when Gruber dissected puppies he did find the *fabellae* prefigured. We have repeated this observation, and we have also found that the kitten at birth prefigures the lateral *fabella* and *cyamella* by nodules of *hyaline*, not fibrous cartilage.

† "Monographie über die aus wahren (hyalinschen) cartilagines praeformirten *Ossicula sesamoidea* in den Ursprungssehnen der Köpfe des *M. gastrocnemius* bei den Menschen und bei den Säugethieren." *Mémoires de l'Académie impériale des Sciences de St Pétersbourg*, VII^e Série, Tome XXII, 1875, No. 4.

Wenzel Gruber starts by telling us (1875) that the *fabellae* in man have been known for 319 years, which gives us closely the date of the 1555 edition of Vesalius' work, and that those of the mammals have been known for 313 years, which is a close approximation to the date of Eustachius' work (permission to print 1562, issued 1564). There is no reference to Sylvius' commentary on Galen's *De ossibus* (see our p. 12). Gruber at once sweeps away the statements that *fabellae* occur always in man, that they occur only or occur occasionally on the mesial side, that they are produced by stress or by friction, or that they occur most frequently in the aged or in males*. While an osteoma may and does occur in the head of both *M. gastrocnemii* it is far rarer than the true sesamoid and does not occur in the same situation. The origin of the *fabellae* is normal and perfectly analogous in the mammals and in man. Gruber then gives the statistics of his observations, to these we shall refer later; they are rather obscurely expressed, Gruber not having a keen sense for figures. We shall refer here only to a few points which bear on his general conclusions. He says that for many years he examined the cadavers of human embryos in last month (total *not* stated), new-born children "in considerable number," "several" children aged one to seven and never in any of these nor in two five year old boys or in one seven year old girl did he find in the tendons of *M. gastrocnemius*, a *cartilago hyalina*, or *fibro-cartilago*. The wording does not strike one as referring to very copious material and possibly the material was inadequate for a *negative* conclusion. In 44 cadavers 10 to 17 years Gruber found only the *hyalina cartilago* as hemisesamoid; in 426 cadavers 18 to 83 years he found only ossified *fabellae*, the orthosesamoids. In the external head he found only *ossicula sesamoidea* and hyaline *cartilagines sesamoideae* (our orthosesamoids and hemisesamoids), never *fibro-cartilagines* or pathological ossifications (pseudosesamoids†). In the internal head none of these occurred except a single pathological ossification, which he figures in Table III, Fig. 3 *g* (see our Plate IV, Fig. 8) and this would never be confused with a true *fabella*. From these data he concludes that (i) neither hemisesamoid nor orthosesamoid occur in the mesial head of *M. gastrocnemius* (p. 67), (ii) there is no trace of a sesamoid in the lateral head in the case of man before 10 years of age (p. 70), and (iii) orthosesamoids originate in a hyaline *cartilago* never a *fibro-cartilago* (p. 68). In other words our hemisesamoid according to Gruber is always hyaline and not fibro-cartilaginous. Here we think Gruber's lesser faults appear. He dogmatically asserts the non-appearance of hemisesamoid or orthosesamoid on the mesial side. He simply discards the records of other anatomists because his own large but necessarily limited experience has not confirmed theirs*.

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* The existence of *fabellae* in man is wholly independent of age and occupation and does not arise from friction (p. 69).

† Pathological ossifications in *M. gastrocnemius* are very rare in man and when they do occur are never in the neighbourhood of articular condylar surfaces, but in head of tendon close to femur and so removed far from site of *fabella* in man (p. 68).

Again in new-born mammals he admits that hyaline cartilaginous *fabellae* are to be seen (pp. 69—70) "as small faint points or streaks macroscopically visible," and yet he asserts that no traces of the *fabellae* are to be found in man before 10 years of age, although elsewhere he emphasises the point that the *fabellae* in man and the lower animals are "völlig analog." We believe that sparsity of material and the comparative ease with which when they do occur (as anomaly) they would escape notice probably account for the discrepancy. The statement that orthosesamoids are always prefigured by hyaline cartilaginous hemisesamoids is very definite and emphasised in the very title of Gruber's paper. All statements as to sesamoids arising from ossification of fibro-cartilage are Gruber tells us incorrect (p. 68). If Gruber be right then we have another and striking instance of how erroneous statements are still perpetuated in the history of sesamoids. For Pfitzner writing only 17 years later, and referring to Gruber's memoir† as a classic of the subject still speaks of our hemisesamoids as developing from "faserigen Gewebe" (S. 563), and even as late as 1897 in the *Seventh Report of the Committee of Collective Investigation of the Anatomical Society of Great Britain* we find sesamoids divided into two classes: "firstly those in which the bodies are osseous, and secondly those in which they were of some other material (fibrous, fibro-cartilaginous, or cartilaginous)‡. Thus if Gruber's statement be correct, it has not got current in the course of 20 years in English anatomy; if incorrect, not even as accurate a German as Pfitzner thought it desirable apparently to issue a formal contradiction! Yet Gruber wrote in 1875 that true sesamoids are always prefigured by the existence of hyaline cartilage, never by fibro-cartilage (p. 65). This prefiguration, he tells us, had not been previously noted in man, and had not been adequately emphasised in mammals generally. All statements as to sesamoids arising from ossification of fibro-cartilage are incorrect (p. 68). Surely such a statement from such an authority deserved at least a contradiction if incorrect?

Yet the anatomists still talk glibly of the origin of sesamoids by intensive stress in fibro-cartilage, and it is left to biometricians to confirm or confute Gruber! We were not able to make an intensive investigation, but we pursued two lines of research.

(i) We had sections taken of the *fabellae* and the *cyamella*, or rather of the nodules where we should suppose them to be, of a kitten at birth. The lateral *fabella* and the *cyamella* exhibited a kernel of hyaline cartilage. We were less successful in our sections of the mesial *fabella*, either it was absent, or else the very small prefiguration of it had been ejected in the sectioning as one or two cavities were visible in the section. Either alternative is possible as the nodule is much harder than its environment and the knife may slip on it, and again, not only is the mesial *fabella* not infrequently absent in the cat, but it develops far less rapidly than the lateral.

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* All statements during 319 years of the existence of a mesial *fabella* in man are "durchaus irrige" (p. 67), Gruber even goes so far as to assert that owing to the *Bursa mucosa supracondyloidea interna* (discovered by him) the internal *fabella* in man would be rather harmful than valuable if it occurred in the neighbourhood of this *bursa*, and if some 2 cms. higher than the external *fabella* would be useless (p. 68). This appeal to "use" is odd.

† Pfitzner gives the wrong volume T. XXIV instead of T. XXII of the St Petersburg memoirs as the locus of Gruber's monograph.

‡ See also Humphry, Quain and other English anatomists for the fibro-cartilaginous sesamoid.

(ii) We asked Professor Elliot Smith if he could provide any information as to the origin of sesamoids in general from a human foetus. The *fabella* and *cyamella* not being universal in man the patella and a metatarsial sesamoid were selected. He placed the matter in the hands of Mr R. B. Green, who has most kindly sent us the accompanying report.

Note on the Histology of Sesamoids in the full-term human Foetus.

Longitudinal sections through the developing sesamoid bone in the tendon of the *Flexor brevis Hallucis* show the cartilage to be essentially of the hyaline variety. At the periphery of the cartilaginous nodule a narrow transition zone between the cartilage and the surrounding young connective tissue may be seen. In this zone fine fibres are interspersed in and gradually fade away into the hyaline matrix. Other fibres pass round the periphery of the cartilage from one extremity to the other.

Longitudinal sections of the patella in the full-term foetus show a similar arrangement in which those fibres which are a continuation of the proximal to the distal tendinous attachment on the surface of the cartilage are more marked.

It will thus be seen that independent lines of investigation confirm Gruber's statement and there is little doubt that if it holds from cat to man, we are fairly safe in asserting that sesamoids are always prefigured by hyaline cartilage*.

The importance of this conclusion is very great. If sesamoids are always prefigured by hyaline cartilage, and do not appear without this origin, and further if this origin can be detected in the foetal state, it is clear that the presence or absence of hyaline cartilage in the foetal state is the condition for the presence or absence of either hemisesamoid or orthosesamoid; and the theory that they are produced by intensive stress or friction falls to the ground, unless it, indeed, be asserted that such factors have produced antenatally the hyaline cartilage nodule! Unless fibrous cartilage could first be converted by stress into hyaline, it is hopeless to maintain that such stress could produce sesamoids. But a study of the regions intermediate between fibrous and hyaline cartilaginous areas appears to indicate that, while there is a form of cartilage which is neither and yet may become either, the one is not an antecedent of the other. In our Plates XVII, XVIII are shown (i) the section of the kitten's *cyamella* and the enlargement of the hyaline cartilage, (ii) the section of the kitten's lateral *fabella*, (iii) the section of the metatarsial sesamoid in the human foetus and (iv) the section of the foetal human *patella*. A more complete study of such material would we believe be of great interest. At present we are only concerned with the fact that the master-craftsman was correct and the text-book writers, who still cling to mediaeval traditions and hypotheses, are wrong.

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* Since the above words were written, we have been able to confirm Gruber's statement in the case of the dog, the rabbit, and other mammals. The results will be discussed in the next instalment of this memoir.

While Gruber asserts the universal absence of the mesial *fabella* in man, he draws attention to the fact that in other mammals the nature of the mesial is differentiated from that of the lateral. Lateral *fabellae* may always occur without mesial; or the mesial may occur occasionally; but there is no type of life in which the mesial always occurs without a lateral *fabella*. This differentiation both in man and other mammals between mesial and lateral *fabellae* is very significant and should find its expression in any theory of origin*. Among other points dealt with by Gruber are the shapes and sizes of the *fabellae*. He divides them into 20 shapes to which he gives mathematical terminology, the most common being tetrahedra, cones, half ovals, four-sided pyramids, oval or circular plates or discs. There is no mathematical accuracy in these descriptions, see for example his Table IV, Figs. 9 and 10 (which he calls a three sided pyramid form!), pp. 30–31. All that we can say is that the *fabellae* are very variable in shape, and that they may be pyramidal as in the marsupial type, or lens-form even to spherical as in the apes, and this only in the roughest resemblance. The "base" is usually smooth. It seems to us that the shape largely depends on the number of muscle-attachments of which the *fabella* is in any case the node, but this point is not emphasised by Gruber. On pp. 35–38 certain measurements are given. The greatest weight of any human *fabella* was 0·847 gr. and the smallest weight 0·009 gr. In the greatest tetrahedral form the height was 13·5 to 14 mm. and the base is given as 10 mm. diameter.

We now come to a most interesting consideration of the *locus* of the external *fabella* in man. Gruber gives three situations for the gastrocnemic ossicles in man. The first of these (p. 38) is the *sulcus popliteus externus*! Now if the reader will examine the case described by Gruber on his p. 38 and illustrated in Fig. 1 of his Table I† (see our Plate V, Fig. 10) I think he will agree that it is no *fabella* at all, but a true *cyamella* and probably most of the pyramidal *fabellae* described by Gruber are really *cyamellae*. Now both *fabella* and *cyamella* occur simultaneously in the knee-joints of many genera and are frequent in the apes. Hence it is remarkable that Gruber should have overlooked this important distinction, and confused a sesamoid occurring in the *depth* of the *sulcus popliteus externus* (p. 71) with a *fabella* of the tendon of the *M. gastrocnemius*. Gruber even tells us that the hump due to this sesamoid can be so large that it can be mistaken for an exostosis; in the extended leg the hump can be so great as to be felt or even *seen*‡ (p. 71). Now there is, perhaps, more reason for this confusion than appears if we loosely speak of the *fabella* as lying in the tendon of *M. gastrocnemius* and the *cyamella* as in the tendon of *M. popliteus*.

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* Confirmation of this differentiation of origin of the *fabellae* is to be found (i) in the fact that the two *fabellae* are not equal in size. It is possible that in the apes the mesial may occasionally be larger, but in all other species it is smaller and frequently much smaller, (ii) the position of the *fabellae* is often different, (iii) ossification of the external *fabella* begins and ends sooner, (iv) the mesial more often than the lateral fails to ossify, and (v) the microscopic structure may be different.

† This figure represents what is almost certainly a *cyamella* embedded in *M. gastrocnemius*, *Ligamentum popliteum* and short external lateral ligament.

‡ "Der Höcker von dem Ossiculum oder der Cartilago wird 2·6—4·2 cms. (in medium 3·325) über der Spitze der mittleren, höchsten Zacke als dem höchsten Punkte des *capitulum fibulae* gefühlt oder sichtbar" (p. 39).

We have already prepared the reader by citing Cheselden and Humphry (see our pp. 18, 21) for such not being the case; both *cyamella* and *fabella* are or may be the node, "Knotenpunkt," or junction of a whole network of fibrous structures, tendons and ligaments. Thus Gruber himself tells us (p. 69) that the lateral *fabella* is at the junction of *M. gastrocnemius externus* and the *Ligamentum popliteum* at the point before *M. gastrocnemius* is free of the knee-capsule and where the short lateral ligament takes its departure. For this reason Gruber asserts that the external *fabella* serves (i) to strengthen this junction, (ii) to keep the "Knotenpunkt" on the articular surface of the condyle, and (iii) to prevent *M. gastrocnemius externus* slipping on to the lateral face of the external condyle. This explanation does not seem to us of great validity for if the *fabella* were of such great service, how would nine-tenths of the human population get on without it? But this conception of the *fabella* as a node to which there are many muscular attachments not only accounts largely for its variety of form, but also leads us to seek for its origin in something to which such muscular attachments were peculiar.

Another most suggestive point here is that Gruber noticed occasionally a supernumerary head* of *M. popliteus* (see our p. 22 and our Fig. 9, Plate IV) springing directly from the *fabella*. Thus the two heads of *popliteus* are brought into touch with the two lateral sesamoids and this division of the head is not inconsistent with the division of an original structure. Gruber's confusion of lateral *fabella* and *cyamella* has in itself a slight contributory significance.

More than once Gruber speaks of the controlling power of the *fabella* whether orthosesamoidal or hemisesamoidal over the ligaments and tendons. Thus on p. 72 he notes that in man its movements control: *M. gastrocnemius externus*, *M. plantaris*, *M. semimembranosus*, and *M. popliteus biceps* by means of its supernumerary head supposing this abnormal muscle present†. Whenever both *M. plantaris* and the *fabella lateralis* exist in man, a portion of the former, or the whole of it, originates in this sesamoid (p. 45). In short in the case of man in the extended position of the limb tendons (*gastrocnemius, popliteus, plantaris*) and ligaments (oblique popliteal, and short external lateral) all united to the sesamoid hold it *in situ* on the posterior surface of the external condyle, near, or on, or in rare cases projecting over the outer condylar border (pp. 46—71).

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* On seven occasions this supernumerary head sprang from the *fabella*; on four occasions without a sesamoid this anomalous head originated from the head of the oblique popliteal ligament, or and also from the knee-capsule, pp. 45—6. We think, but it is not quite clear, that Macalister (see our p. 22) also had associated the supernumerary head of *M. popliteus* with a sesamoid. See also J. F. Knott, *Proc. R. Irish Academy*, Second Series, Vol. III, p. 639, 1882.

† Again p. 48 we read: "Da nun das Ossiculum und die Cartilago gerade im Knotenpunkte der Vereinigung der Kniekapsel, der Sehne des *Gastrocnemius externus*, des *Lig. popliteum* und des *Lig. laterale externum breve genu* sitzen, da von denselben der *Gastrocnemius externus* mit Fleischbündeln abgehen kann, immer der *Plantaris* davon entspringt, oder falls er fehlt, durch von da kommende Fleischbündel des *Gastrocnemius externus* ersetzt wird, bisweilen von denselben der *Popliteus* mit einem supernumerären Kopfe entspringt; so werden auch diese Muskeln die Verschiebung des *Ossiculum* und der *Cartilago* dirigiren, und es werden durch denselben Apparat, durch den die im Bereiche des *Condylus externus* laxere Kniekapsel vor Einklemmung geschützt wird, auch das *Ossiculum* und die *Cartilago* vor Einklemmung bewahrt. Beide werden bei diesem Manöver, und bevor es zur grössten Spannung kömmt, schräg ein—und aufwärts an dem *Condylus externus*, wenn auch nur eine mässige Strecke, gleiten müssen, um der Einklemmung zu entgehen, und bei der Streckung des Kniegelenkes wieder auf ihren Platz auf demselben Wege zurückkehren."

The reader will recognise what an enormous stride the master-craftsman made in thus investigating the muscular attachments of the *fabella lateralis* in man! Yet even to-day the anatomical text-books content themselves by describing this sesamoid as occasionally occurring in the external head of *M. gastrocnemius*,—a rough description as old as the mid 16th century—and suggesting as Galen did that, as a sesamoid, it is scarcely worthy of study. If we disregard, as we think we must, Gruber's theory of the purpose of the *fabella lateralis* and his identification of the *cyamella* with this sesamoid, we have still to trace the origin of these muscular attachments and the undoubtedly close relations of these two sesamoids. If we discard the first *locus*, i.e. the popliteal sulcus, which Gruber gives to the *fabella lateralis* in man, we find him recording two alternatives*.

(i) Embedded in fibrous structures. The place of the embedment is the posterior wall of the knee-capsule where the tendon of *M. gastrocnemius externus* unites with the oblique popliteal ligament and with the origin of the short external lateral ligament or the partial union of some of these and the knee-capsule itself (pp. 39—40).

(ii) In a facet or groove on the condylar articular surface generally near the border. This facet is either flat or slightly concave, sometimes saddle-shaped† (p. 40).

In the case of the *fabella* lying in a facet the base in contact with the facet has according to Gruber no cartilaginous covering. In the case of the *fabellae* of all mammals—*Gulo vittalus* excepted—the base where they articulate has a cartilaginous covering (p. 71).

Accordingly it will be seen that it is hardly accurate to say of the *fabella* and the *cyamella* that the former is found in the tendon of *M. gastrocnemius* and the latter in the tendon of *M. popliteus*. It is more accurate to assert that the latter will be found in the popliteal sulcus, and the former on the posterior articular surface of the condyle, either somewhat removed from it, or in the close contact of a facet. The muscular attachments of both are found to be in part closely similar. Thus Gruber's error in failing to distinguish between the *fabella* and *cyamella* in man, while noteworthy, if he had started from other primates where both coexist, is not so remarkable when he started from the musculature in man, where both rarely coexist.

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* It is singular how very closely Gruber's description of the sesamoid of the popliteal sulcus (our *cyamella*) agrees in its muscular attachments with those of the *fabella lateralis* in its embedment locus. Thus he writes: referring to Fig. No. 4 of his Tafel (see our Plate V, Fig. 10) "Das *ossiculum* und die *Cartilago* liegen im *Sulcus popliteus externus* von fibrösen Gebilden (a, b, d [i.e. Knee capsule, oblique popliteal ligament and short external lateral ligament]) mit welchen sie verwachsen sind, und von Muskelbündeln (k, l, [i.e. *M. gastrocnemius externus, M. plantaris*]) welche von ihnen entspringen umlagert." It will be seen that when both sesamoids are not simultaneously present—as they are in the case of the cat which has both lateral *fabella* and lateral *cyamella*,—there is some reason for confusing the two.

† A flat facet occurs in $\frac{4}{7}$ of such cases, a really deep groove is very infrequent (p. 41).

The bulk of the remainder of Gruber's monograph is taken up with a discussion of the *fabellae* in other living forms than man. He made a long study of the literature of comparative anatomy and added many observations of his own. To these matters we shall return in the following section of this memoir.

Before we leave the topic of the *locus* of the *fabella lateralis* in man we think some study of our Plates I and II is desirable. In Plates I and II, Figs. 1, 4, 5 represent the strange positions of the *fabella* provided by Trew, Heister, and Casserius. Fig. 4 gives the position as envisaged by Camper, while Fig. 5 first shows some daylight as cast on the subject by Humphry*. In Plate I, Fig. 3 we provide a copy of Gillette's representation. It is clearly a case of *Locus II*, the *fabella* resting in a flat facet on the condyle. Plate VI, Figs. 14 and 15 give a knee-joint from the Dissecting-Room at University College, London, to which our attention was drawn by Dr D. E. Derry. It is again a case like Gillette's of a facet *fabella*. The facet lies somewhat high on the articular surface of the condyle. Plate V, Fig. 10 gives Gruber's representation of a sesamoid in the popliteal sulcus. Fig. 12 is a good representation from Gruber of a "Knotenpunkt" *fabella*. Plate IV, Fig. 9 is an illustration of the *M. popliteus biceps* with the supernumerary head attached to the sesamoid; it also shows the short lateral ligament likewise attached and the relation to *M. gastrocnemius externus*. Plate V, Fig. 11 shows the relationship of the *fabella* to *M. plantaris* as pointed out by Cheselden and Humphry, while Plate IV, Fig. 8 gives the only mesial ossicle observed by Gruber, an obviously pathological ossification as he states.

We may say that both *locus* and muscular attachments had been fully studied as far as the lateral *fabella* is concerned by 1876.

(*c*) *Pfitzner's Monograph.* "Die Sesambeine des Menschen." Schwalbe's *Morphologische Arbeiten*, Bd. I. S. 517—762, Jena, 1892. We have already referred to many points of Pfitzner's work (see our pp. 2, 5, 26). He rejected the intensive stress hypothesis and carried the subject a step beyond Gruber by asserting a vestigial rather than a "use" origin. Sesamoid bodies (hemisesamoids) which he considers develop in "faserigen Gewebe" are "Abortivzustande" of sesamoid bones (orthosesamoids), p. 571. He places the *fabella lateralis* on the top and edge of condyle (pp. 568 and 578)—a position in accord with some of Gruber's observations, but differing widely from our own skiagram series. Only in one case (p. 581) did Pfitzner find the *fabella* in a facet on the condyle, which he speaks of as being its original place. While Gruber uses the word "gleiten" = glide, for the action of *fabella* on articular surface of condyle, Pfitzner states that the sesamoid is incapable of moving on the condyle (p. 548), although it is never united (verschmolzen) to the femur.

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* Gruber considers that Weitbrecht and Humphry first placed the lateral *fabella* in its true position. We have already (p. 21, footnote) referred to the grave doubts which arise about what the former intended.

Pfitzner is less dogmatic than Gruber as to the existence of a mesial fabella in man allowing a certain amount of weight to the records of Heister, Morgagni, Hyrtl and Macalister (see our p. 23), but he states that he has never seen it himself (p. 580). On the other hand he has always found it in dog, fox and hare, while in 52 cats he found the *fabella lateralis* always present, but the *fabella mesialis* was absent in 29 out of the 52 cases.

Turning to the *cyamella lateralis,* which Pfitzner describes as in the tendon of *M. popliteus* and working on the curved continuation of the articular surface of the *Condylus lateralis tibiae,* he states that it is constant in *Felidae* and *Leporidae,* and that he has himself *once* found it in a dog. He says that it has never been noticed in man. If we can trust the observations of Macalister, Krause and Knott, and if we have not misinterpreted those of Gruber this statement is inaccurate (pp. 583—584). Lastly as far as we are aware Pfitzner is the only person who has recorded a *cyamella mesialis,* and this only in two cats (p. 584). He was unable to note the muscular attachments. We have gone through a considerable number of dog skeletons in the Biometric Laboratory, in which as a rule the *fabellae* are preserved, but have met with no cases of *cyamellae* being preserved.

The literature of the sesamoids of man is fairly comprehensively treated by Pfitzner, and we have found his references very helpful in our search into the history of our knowledge of the sesamoids in man. We shall refer to his statistics of occurrence in man later. On the whole while Pfitzner's memoir is of great value—in particular he recognised the *cyamella*—it is not epoch-making in the sense of Gruber's.

(5) *Frequency of the Fabellae in Man.*

Putting aside the vague statements of the mediaeval anatomists we have five sources from which this frequency may be determined (i) Gruber, (ii) Ost, (iii) Pfitzner, (iv) the *Seventh Report of the Collective Investigation Committee,* (v) Skiagram Data.

We can dismiss Ost at once; his paper* is very brief and refers to only 30 cases in which he found a *fabella* five times or 16·7 °/₀; sex is not given. Pfitzner observed hemisesamoids or orthosesamoids in 30 out of 290 cases or in 10·34 °/₀. He never met with a *fabella mesialis.* While Pfitzner presents little analysis of his cases Gruber provides a considerable amount, but it is occasionally far from clear as to what exactly he is referring to.

Thus Gruber tells us (p. 70) that without regard to size or sex it appears in about $\frac{1}{6}$ of the cases, i.e. 16·7 °/₀. On p. 26, however, he tells us that in 2340 limbs he found it in 400 instances or 17·1 °/₀. Paying regard to sex Gruber states, again on p. 70, that he found it in about $\frac{1}{5}$ of the male cases and $\frac{1}{8}$ to $\frac{1}{4}$ of the female; according to this the lateral *fabella* occurs in 20 °/₀ of cases in man and

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* Ueber das Vorkommen eines Sesambeines in den Ursprungssehnen des *Gastrocnemius* beim Menschen. *Zeitschrift für Anatomie und Entwickelungsgeschichte,* Bd. II, S. 309, Leipzig, 1881.

25 °/。 to 33 °/。 in woman. Turning back to p. 26 we find that Gruber makes the following statements:

Ages 10 *to* 83* *without regard to sex:*

220 cadavers or 440 limbs, 66 lateral *fabellae*, i.e. 15 °/。.

Sexed Cases:

400 male limbs, lateral *fabellae* in 77 cases,
100 female limbs, lateral *fabellae* in 22 cases,
i.e. Males 19·25 °/。, Females 22·0 °/。.

Extremities, Age unknown. Both sexes:

1400 with 235 lateral *fabellae*, i.e. 16·8 °/。.

Without Age, but sexed:

Male limbs 294 with 61 lateral *fabellae*,
Female limbs 98 with 29 lateral *fabellae*,
i.e. Males 20·8 °/。, Females 29·6 °/。.

Returning to the 2340 limbs, Gruber tells us, however, that (p. 26)

940 male limbs gave 165 lateral *fabellae*,
840 female limbs gave 143 lateral *fabellae*,
i.e. Males 17·6 °/。, Females 17·0 °/。.

Finally we read (p. 27) that

1155 right limbs gave 212 lateral *fabellae*,
1185 left limbs gave 188 lateral *fabellae*,
i.e. Right Limbs 18·4 °/。, Left Limbs 15·8 °/。.

We find it extremely difficult to deduce anything like definite percentages from this tangle of figures, and it would seem that this huge mass of material has been largely wasted for statistical purposes. We can only suppose that the difference of percentages arises from the proportion of young limbs which may be included in the different series.

We may, perhaps, conclude:

(*a*) That there is no significant sexual difference.

(*b*) That there may be preponderance of right limbed lateral *fabellae*.

(*c*) That for all ages and sexes the percentage (judged from 2340 limbs) is 17·1 °/。.

Why this percentage should run up to 22·0 °/。 in the case of sexed femora of unknown age we are unable to say; or, why it should fall to 15·0 °/。 in the case of the 220 cadavers, unless the younger ages have been omitted in the previous result, we cannot explain. Possibly the latter form an earlier part of the record, and that observation became more stringent and accurate as the investigation progressed. The *fabellae* enumerated include both hemisesamoids and orthosesamoids. The results are in rough agreement with Ost's short series, but shew a far higher frequency than Pfitzner's record.

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* The maximum frequencies at the decades indicate that these records of age are very rough.

We now turn to the interesting *Seventh Report of the Committee of Collective Investigation of the Anatomical Society of Great Britain and Ireland for the year* 1896—1897*. We have already commented on the high percentage of lateral *fabellae* reached by Gruber, but these percentages are at least doubled in the statistics of this *Report.* Over 40 $^\circ/_\circ$ of occurrence of *fabellae* are here recorded, and if this rate of increase of percentage continues we shall soon have to return to the standpoint of Vesalius! One wonders (i) if the distinction between limb and cadaver has always been maintained, (ii) if the distinction between condyle and limb has also been maintained†, and lastly supposing the results do indicate the number of *fabellae* per 100 condyles, (iii) if the "Knotenpunkt" itself in which the lateral *fabella* is to be sought has not been occasionally mistaken for a sesamoid‡.

In 287 limbs of both sexes examined, 81 lateral *fabellae* and 39 mesial *fabellae* were found. These figures provide 28·2 $^\circ/_\circ$ of lateral *fabellae* and 13·6 $^\circ/_\circ$ of mesial *fabellae,* i.e. about twice as many lateral as mesial. Now Pfitzner, Gruber and ourselves have not discovered in man any mesial *fabellae.* Hence we must put against Pfitzner's 10·34 $^\circ/_\circ$ and Gruber's 17·1 $^\circ/_\circ$ the 41·8 $^\circ/_\circ$ of the present investigation. But the matter takes a different form if we distinguish between osseous and non-osseous *fabellae*§. Of the 81 lateral *fabellae* only 28 were orthosesamoids; and of the 39 mesial *fabellae* only three were reported as osseous. In other words only 9·75 $^\circ/_\circ$ of orthosesamoidal lateral *fabellae* occur, and 1·05 $^\circ/_\circ$ of orthosesamoidal mesial *fabellae.* These results are very luminous for the controversies of the mediaeval anatomists. Supposing those three mesial orthosesamoids were actually and correctly diagnosed then if the mediaeval anatomists had, as they probably had an osseous body in view they might easily have examined a hundred or more limbs without finding a mesial *fabella.* It is even conceivable that Pfitzner might not find one in 290 limbs. It is less conceivable that they should have escaped Gruber in the case of 2340 limbs, and in the case of both Pfitzner and Gruber who were well acquainted with hemisesamoids, it is surprising that neither found a mesial hemisesamoid in 2630 limbs examined, when they ought to have found 331 on the scale of the *Collective Investigation Report.* It must be quite clear that these different investigators had a totally different conception of the nature of a non-osseous sesamoid, and that this is the origin of the surprising percentage differences we encounter in these investigations as to the presence of *fabellae* in man*. We believe that until the nature of the hemisesamoid has been standardised (for example, it is defined as a hyaline *cartilago* after Gruber, or otherwise), it is unwise to lay stress on any other statistics than those of orthosesamoids.

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* *Journal of Anatomy and Physiology*, Vol. XXXII, p. 182, London, 1898.

† A condyle gives only one chance, a limb two chances, and a cadaver four chances of a *fabella.*

‡ The *Report* says: "With regard to the constitution of the bodies we have evidence that in many of the investigations no microscopical examination was made. We shall therefore content ourselves with dividing the cases in which sesamoid bodies occur into two classes,—first those in which the bodies were osseous; secondly those in which they were of some other materials (fibrous, fibro-cartilaginous, or cartilaginous)," p. 184.

§ It is not, perhaps, adequate to treat these as orthosesamoids and hemisesamoids, as they may contain fibrous structures, which Gruber and probably we ourselves should not class as hemisesamoids.

Out of a total of 79 *fabellae* found in male subjects by the *Collective Investigation* 22 were orthosesamoids, and of 28 *fabellae* found in female subjects 10 were orthosesamoids. Accordingly less than a third of the *fabellae* were osseous, or more exactly the chance of a *fabella* in man being orthosesamoidal is almost ·30. Thus we should expect in the 79 male *fabellae* 24 orthosesamoids and 55 hemisesamoids (as against 22 and 57 observed), and in the 28 female *fabellae* 8 orthosesamoids and 20 hemisesamoids (as against 10 and 18 observed). With a standard deviation in the males of about 4·0 and in the females of about 2·4, the differences of observed and computed are non-significant, or we cannot assert a sex-differentiation in ossification. This *pro tanto* is against an intensive stress theory of origin, for if orthosesamoids are produced by stress from hemisesamoids, we might reasonably expect greater stresses in the male, and a larger proportion of orthosesamoids in their total.

Again in a total of 146 right limbs 61 *fabellae* were found or 41·8 per 100 limbs. In 141 left limbs 59 sesamoids were found or again 41·8 per 100 limbs. It is therefore difficult to accept the statement of the *Report* (p. 186, (2)) that *fabellae* are rather more common on right than left limbs. In 157 male limbs 76 *fabellae* were found or 48·2 per 100 limbs; in 84 female limbs 27 *fabellae* were found or 32·1 per 100 limbs. This shows a greater preponderance of *fabellae* of all sorts in the male, although both sexes have the same ratio of orthosesamoids to hemisesamoids. This result contradicts that of Gruber (see our p. 33, (*a*)) and appears opposed to the conclusion drawn by the framer of the *Report* (p. 186) himself, who writes: "sex has little influence on their [i.e. the *fabellae's*] frequency."

The chief value of the statistics† in this *Report* is the confirmation they

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* Again on the scale of the *Collective Investigation Report*, Gruber and Pfitzner between them ought to have found between 26 and 27 mesial orthosesamoidal *fabellae*. They found *none*. Hence we are compelled to suppose either racial differences exist in this respect, or that one or other set of observers is in error.

† A further point is worth recording, namely the correlation between the appearance of *fabellae* in both heads. Clubbing together both sexes and both sides we have 241 limbs showing the following table:

Presence of *Fabellae* in the two Heads of *M. gastrocnemius*.

		Outer Head.		
		Present	Absent	Totals
Inner Head.	Present	13 (10)	20 (23)	33
	Absent	57 (60)	151 (148)	208
	Totals	70	171	241

provide of the occasional occurrence of mesial orthosesamoidal *fabellae* as asserted by Hyrtl, Macalister and others. But even assuming the correctness of the observation we are forced to the conclusion, that mesial orthosesamoidal *fabellae* are very rare in man, that mesial hemisesamoids are also much rarer than lateral, and that generally man confirms the view that there is a marked differentiation in origin between the lateral and mesial seasamoids of the knee-joint.

(6) *Skiagraphic Data for the Occurrence of the Sesamoids of the Knee-Joint in Man.*

Our data in this case consists of (i) 102 skiagrams of the knee-joint taken at a military orthopaedic hospital and examined by the kindness of Dr Stanley Melville, and (ii) 352 skiagrams of the knee-joint, which were found among the thousands of skiagrams taken at the Fulham Military Hospital and now deposited at the Royal College of Surgeons. We owe to the kindness of Professor Keith our access to this material. Dr Melville found seven cases of the presence of lateral *fabellae*, we found 22 certain cases and a doubtful four further cases. The results 6·9 °/ₒ and 6·2 °/ₒ to 7·4 °/ₒ are in very good agreement. We think it safe to conclude that skiagraphically visible *fabellae* occur in about 7 °/ₒ of human cases. If we suppose (i) that hemisesamoids would not show on the skiagrams and that (ii) they are twice as numerous as orthosesamoids we should reach about 21 °/ₒ as the occurrence of the lateral *fabella* in man, i.e. a percentage approximating to Gruber's and that of the *Collective Investigation Report*, but much in excess of Pfitzner's. Dr Stanley Melville was not able to report a single case of the appearance of two *fabellae*, although there is a shadow on one of his plates (see our Plate XV, Fig. 33) which by a great stretch of the imagination might possibly be interpreted as a second *fabella*, much more distally situated than is customary. In the skiagrams from the Fulham Military Hospital we have not succeeded in finding any trace of a mesial *fabella*. Yet if the data of the *Collective Investigation Report* are to be trusted we ought to have come across five to six mesial orthosesamoids in the total of 454 limbs; we do not refer to the hemisesamoids for we assume they would not appear in skiagrams. Now while we cannot disregard the statements of such qualified observers as Hyrtl and Macalister, and dogmatically assert with Gruber that a mesial *fabella* has no existence in man, we feel bound to say that we feel it exceedingly elusive, and that we must emphasise the importance of the next recorder preserving an anatomical

If we apply tetrachoric computation to this table—and the variety in size and constitution of the *fabellae* roughly justifies it—we find for the correlation

$$r = {\cdot}1790 \pm {\cdot}0885.$$

We see at once that there is no close and significant relation between the appearance or absence of *both fabellae* simultaneously, i.e. there is no close organic relation between them in man. In fact if distributed purely at random we should anticipate 10 cases in which mesial and lateral *fabellae* would appear simultaneously. We give the numbers which might be anticipated if the appearances were absolutely independent in brackets. This approach to independence in origin is certainly singular in the case of man, considering the universality of *fabellae* in so many lower types of life.

preparation, and further urging all able to do so to examine carefully skiagrams of the knee-joint, recording not only presence but absence of one or both *fabellae**.

The skiagrams give very accurately the position of the *fabella* with extended limb. That position is opposing the middle third of the posterior face of the lateral condyle. Generally we may say that while it is sometimes more proximal or more distal, it stands midway opposite to the vertical wall of the articular surface. As our skiagrams are not stereoscopic it is impossible to hazard any statement how far the *fabellae* are removed from the midplane of the condyle towards the lateral border of the articular surface. Our diagrams show what great variation there is in the size of these sesamoids.

In seven of our illustrations (Plates VII, VIII, IX, XV, XVI, Figs. 16, 17, 19, 20, 32, 33, 34) the *fabella* shows complete separation from the articular surface of the condyle; it is extremely unlikely that a facet could exist in these cases, and certainly not a grooved facet. In possibly three cases only (Plates VIII, IX, XVI, Figs. 18, 21, 35) is it reasonable to suppose that facets may have existed; in these three cases, however, it is hardly reasonable to suggest that the sesamoid is in the least depressed below the articular condylar surface. It would thus appear that the first of Gruber's positions for the *fabella*, i.e. embedded in the node of fibrous structures, is about, very roughly, two to three times as frequent as his second position, i.e. situated in a facet on the condylar articular surface.

Plate XV, Fig. 33 is the case we have already referred to (p. 36) in which there is some sign, still very elusive, of a second *fabella*. We are unable to lay any stress on it. It will be at once recognised that the drawings of Trew, Heister and Casserius hardly describe anything which appears in our skiagrams.

We may now draw attention to sesamoids of the knee-joint appearing in somewhat anomalous positions. Plate XIII, Fig. 29 shows apparently two small sesamoids opposing the lateral face of the external condyle, but somewhat removed from its surface. Plate XIV, Fig. 31 gives with less certainty a single sesamoid in a somewhat similar situation. The roundness of these individuals appears to preclude any pathological origin. They are too high up to represent in any way normal *cyamellae*. They might almost be described as intermediates in position between *cyamella* and *fabella*. Their almost vertical position over the head of the fibula is not without suggestiveness. But without evidence from the dissecting-room, or confirmatory skiagraphic records, we wish neither to assert that there is a third position possible for the *fabella*, or that occasionally an additional sesamoid of the knee-joint may occur in a position intermediate between that of *fabella* and *cyamella*. We know of no such sesamoids in lower types of life; for the time being we may call them x-sesamoids and if in the future no further evidence is forthcoming with regard to them, they may be dropped. We did not, however, like to pass them by without a word of record.

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* We shall be extremely grateful for any material with regard to sesamoids of the knee-joint which may be sent to us (Biometric Laboratory, University College, London, W.C. 1).

Cyamella in Man. It is very much less easy to differentiate the *cyamella* by aid of skiagraphic analysis. As it lies deep in the popliteal sulcus, it can hardly be distinguished by a *norma lateralis* of the knee-joint. A *norma frontalis* provided the *cyamella* is of considerable size appears to give the best chance. Thus Plate XI, Fig. 25 provides an illustration of what is probably a *cyamella lateralis.* Plate X, Figs. 22 and 23 shows another *cyamella lateralis* from posterior and frontal aspects. Plate XI, Fig. 24 gives our nearest approach to a *cyamella mesialis.* There is something similar in Figs. 22 and 23 of Plate X. We decline to interpret them and should refuse entirely to be dogmatic about them. But taken in conjunction with Pfitzner's statement as to what he had found in two cats (see our p. 32), we think it important that in the dissecting-room, the skiagraphic studio and the laboratory of comparative anatomy the investigator should bear in mind the slight possibility of a *mesial cyamella**. We have found two probable and one doubtful lateral *cyamellae* in our 352 cases, or in 0·57 °/₀ of cases probably and in 0·85 °/₀ possibly. Thus the *cyamella lateralis* in man first recorded by Macalister appears to be of great rarity.

Lunulae. Our search for these sesamoids so common in lower types was not very successful. In the first place the skiagrams do not exhibit ossifications of the semi-lunar cartilages at all clearly, and in the next pathological ossifications of the semi-lunar cartilages appear to be far from infrequent. Plate XII, Figs. 26, 27 and Plate XIII, Fig. 28 indicate what may be true ossicles of the semi-lunar cartilages. In the case of Fig. 27 the *lunula* is accompanied by what may possibly be an ossicle on the antero-lateral border of the tibia immediately above the *capitulum fibulae.* On the whole we found nine *lunulae* ranging through various shades of doubtfulness. Thus the occurrence of *lunulae* in man does not exceed 2·5 °/₀ of knee-joints *and is probably far less.*

We have not included the *patella* in our consideration of the knee-joint sesamoids, but in examining these skiagrams we have found apart from obvious pathological cases five or six of double *patella*†. We are prepared indeed to be told that even these six are pathological ossifications of the tendon of the quadriceps. But we are not equally certain that those who will take this view are fully aware of the regular occurrence of the double *patella* in certain lower types. Tillmans and Bernays‡ have found in man in several cases a hemisesamoidal body above the true *patella* and Bernays notes the same conditions in some of the *Felidae* and the rodents (Cat, Mouse, Rabbit). Pfitzner found such a double *patella* in the *Leporidae* (*loc. cit.* S. 577). In this consideration it is worth noting that *Macropus giganteus* has a hemisesamoid instead of an orthosesamoid for its *patella*. Our Plate XIII, Fig. 28 and Plate XIV, Fig. 30 show typical cases of such double *patellae* in man. We suggest that in discussing the pathological nature of these cases, the possibility that they have vestigial associations should not be entirely overlooked*.

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* In the first and last cases an anatomical preparation should certainly be preserved of any discovery or supposed discovery. Our own case is not so definitely an osteome as Gruber's: see our Plates X and XI, Figs. 22—24.

† No percentage is possible as the anterior and posterior views of the knee-joint give no power of discriminating a double *patella.*

‡ "Die Entwicklungsgeschichte des Kniegelenkes," *Morphologisches Jahrbuch,* IV, Supplement, 1878, S. 442.

(7) *Summary of our Knowledge as to the Sesamoids of the Knee-Joint in Man.*

After 19 centuries of consideration, 18 of which were little better than fumbling, we can sum up our present knowledge of these sesamoids as follows:

(*a*) An orthosesamoidal lateral *fabella* occurs in man in about 7 °/₀ of knee-joints.

(*b*) In two to three times this number of cases there is a hemisesamoid, probably if indeed not almost definitely a hyaline *cartilago*.

(*c*) The situation of this *fabella* in about three-fifths of the cases is roughly opposed to the articular surface of the condyle near its most posterior point, but separated from it by 3 to 7 mms. It is the "Knotenpunkt" of a variety of muscles. In about two-fifths of its occurrences the *fabella* lies on a facet upon the articular surface of the condyle.

(*d*) There is some evidence for the far rarer existence of a mesial orthosesamoidal *fabella*, but both the evidence and this *fabella* itself are very elusive. The *Collective Investigation Report* records it in about 1 °/₀ of knee-joints. Gruber did not find a single case in 2340 knee-joints, and we have only found a single and very doubtful trace of it in 1 out of 454 skiagrams of the knee-joint. The same *Report* asserts that there are 13 times as many mesial hemisesamoidal *fabellae* as orthosesamoidal. Gruber again, and Pfitzner also, record none whatever. Macalister and Hyrtl and others have recorded their presence.

(*e*) The lateral *cyamella* has been reported by Macalister in man. We believe that we have found it in under 1 °/₀ of skiagrams of the knee-joint. If we interpret Gruber's statements correctly, he has erroneously termed the sesamoid he found in the popliteal sulcus a *fabella*, it should be a *cyamella*, and this is further evidence of its rare appearance as an anomaly.

(*f*) The existence of a mesial *cyamella* in man cannot be said to be established by the few doubtful skiagrams we have reproduced (Plates X and XI). Mesial *cyamellae* do not occur in any family of mammals universally. Pfitzner reports two cases in the cat, which always has a lateral *cyamella*. The sole interest of the anomalous appearance of a mesial *fabella* would be to strengthen the possibility that an organ which is persistent on one side of a limb may anomalously reduplicate itself on the other.

(*g*) There is some slender evidence of the rare occurrence of *lunulae* in man. They have not as far as we are aware been systematically sought for in the dissecting-room. We should expect them as rare anomalies in man as they exist universally in certain lower forms.

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* In the Fulham series of skiagrams also occurred four well marked cases of Gruber's *Processus supracondyloideus ossis femoris*: see Pearson and Bell, *Monograph on the English Longbones*, Part I, The Femur, Text pp. 85—89, and Atlas, Plates XXVI—LXVIII.

(*h*) Three hypotheses have been provided for the existence of the sesamoids of the knee-joint, namely:

(i) The theory of their manufacture from cartilage by intensive stress or even by friction. Against this hypothesis it is adequate to cite the cartilaginous *patella* of the giant kangaroo, the persistent *fabellae* of the smaller primates, and the relatively rare occurrence in man, the persistent *lunulae* of the squirrel and the absence of *lunulae* except as anomalies in man; the fact that the male has no higher percentage of *fabellae* than the female, and the general absence of *fabellae* in the greater and more massive anthropoids.

(ii) The theory that the lateral *fabella* serves a useful purpose as strengthening the "Knotenpunkt" of a congeries of muscular attachments. Such a hypothesis of use value might be valid, if man were a living form developing for the first time a *fabella*. On the contrary more primitive types of the primates have it universally and the higher types appear to have lost it or at least to be losing it. If the lateral *fabella* in man was there because it was of great service it would be difficult to explain why 7 °/₀ need it and 93 °/₀ get on very well without it!

(iii) The theory that the *fabellae* and the *cyamellae* are vestiges of some structure of earlier form, which has disappeared, and that hemisesamoids are not stages towards orthosesamoids, but the last steps in a degenerative process. Any such theory of the sesamoids of the knee-joint if valid will have to account for the marked differentiation in frequency, size and constitution of lateral and mesial sesamoids, and it will have to give some account of the structure of which they may be supposed to be the debris. It will also have to account for the muscular attachments of the sesamoids which we now find associated with the knee-joint in man.

This third hypothesis seems to us the only reasonable one hitherto proposed for the existence of the sesamoids of the knee-joint, and we shall therefore endeavour to trace the evolutionary history of the *fabella* and *cyamella*. If we observe that in the earlier primate forms the sesamoids of the knee-joint are osseous, we can dismiss the question of hemisesamoids; the only account we need give of them is that they are a measure of the extent of degeneracy, signposts to where an orthosesamoid once existed, and not the beginnings of sesamoids awaiting old age or intensive stress to make them osseous. We turn now to a study of the sesamoids of the knee-joint in living forms other than man, endeavouring to combine our own observations with those occasionally contradictory *inter se* of other observers.

DESCRIPTION OF PLATES.

The first five plates represent historically the development of the anatomists' conception of the sesamoids of the knee-joint.

Plate I. Fig. 2 shows after Pfitzner the sesamoids of first metatarsal of the foot in man. Such sesamoids of the digits were certainly known to the Greeks. They are the most conspicuous and we cannot demonstrate that the Greeks knew those of the knee-joint. It is reasonable to suppose that the seed of the plants the Greeks called sesamé should somewhat resemble these sesamoids.

Fig. 1. First drawing of the *fabellae*. It occurs in Casserius' *Tabulae anatomicae* of 1632 which illustrate Adrian Spiegel's *De humani corporis fabrica*. The latter following Vesalius asserts the existence of sesamoids in *both* heads of the external *gastrocnemius*, and they are thus somewhat naively exhibited by Casserius. There is no trace of the "Knotenpunkt" of actuality.

Fig. 3. See under Plate IV.

Plate II, Fig. 4. Diagram from the Altorf 1715 dissertation, *De chylosi Foetus in utero*, of C. J. Trew. The diagram shows none of the muscular relationships of the external *fabella*. F. V shows the sesamoid resting in what Trew thought its customary situation, "os sesamoideum insidens cavitate condyli exterioris in omnibus femoribus conspicuae." F. VI exhibits "os sesamoideum femoris magnitudine naturali extra situm." Trew makes no reference to an internal *fabella* in his supposed discovery. The "conspicuous cavity in all femora" appears to be the roundish impression for the insertion of the lateral head of *M. gastrocnemius* on the external epicondyle, a situation where the sesamoid is not in our experience ever found.

Fig. 5. This drawing is taken from Laurence Heister's *Compendium Anatomicum*, Edition 1748. There is much in it to indicate that Heister notwithstanding his paper of 1717 (see our p. 18 ftn.) copied Trew's illustration, but added the mesial *fabella*, which he rests on the horizontal surface of the condyle in immediate association with the supracondylar tubercle.

Plate III, Fig. 6. Peter Camper's drawing of the external *fabella* from his 1754 memoir: "Vom Bruch der Kniescheibe und des Olecranon" (S. 68 of the *Vermischte Schriften* of 1801). *AKIL* is the tendon of the outer head of *gastrocnemius* "worin sich ein Knöchelgen (*ossiculum sesamoideum*) *f. g.* findet, welches man in dem inneren Bauch derselben nie sieht." *f. g.* is not marked on the figure, but is presumably the shaded portion. If so, the relation of this sesamoid to the other muscles and ligaments is far from clearly indicated.

Plate IV, Fig. 7. A drawing after Sir George M. Humphry's figure in his *A Treatise on the Human Skeleton*, 1858 (Plate LI, Fig. 2). Posterior view of left knee-joint, described as follows: *A*, *ligamentum posticum*; the thickest portion of it ascends from *B* the *semimembranosus* to *C* the outer head of *gastrocnemius*. *D* a sesamoid bone at its junction with the latter. *E* inner head of *gastrocnemius*, also connected with *ligamentum posticum*. *F* popliteus muscle, raised a little to show *G* the posterior peroneo-tibial ligament. *H* external lateral ligament. Humphry thus indicated the relation of the sesamoid to the *ligamentum posticum*.

Fig. 3 of Plate I (placed there for economy of space) is from the historical order to be considered here. It is copied from Gillette's memoir of 1872 (see our p. 23). *a* is the external *fabella in situ*, *b* the *gastrocnemius* and *c* the situation where it rests on the posterior surface of the condyle. The situation is fairly in accordance with that suggested by Humphry, but Gillette does not indicate the relationship of the sesamoid to other ligaments and muscular attachments.

Figs. 8 and 9 of Plate IV and 10, 11, 12 of Plate V are all taken from W. Gruber's great memoir of 1876, which is the first to illustrate carefully the muscular attachments to the sesamoid.

In all these figures 8 to 12, except Figs. 9 and 10 where by an unfortunate slip of the engraver 5 has been placed for δ, the system of lettering is the same, namely:

1 = femur, 2 = tibia, 3 = fibula, 4 = sesamoid. *a* = knee-capsule, *b* = *ligamentum popliteum*, *c* = long external lateral ligament or *ligamentum anticum*, *d* = short external lateral ligament, or *ligamentum posticum*, *e* = external *meniscus genualis*, *f* = great adductor muscle, *g* = *M. gastrocnemius internus*, *h* = *M. semimembranosus*, *i* = *M. biceps femoris*, *k* = *M. gastrocnemius externus*, *l* = *M. plantaris*, *m* = *M. popliteus*,

n=*M. popliteus biceps* (Fig. 9), o=internal supracondylar tubercle, p=*processus tuberositatis* of the internal condyle for the insertion of the tendon of the adductor muscle, γ=superficial and δ (engraved 5 in Figs. 9 and 10)=deeper layers of the under "strängformig" portion of the tendon of origin of *M. gastrocnemius externus.*

Fig. 8 shows the only mesial *fabella*, 5, observed by Gruber; it was a pathological ossification, α being the upper vertical, and β the transversal limb of this pseudosesamoid; it appears to be associated with a somewhat emphasised tuberosity of the internal condyle, p.

Fig. 9. A most interesting illustration of the anomaly of *M. popliteus biceps*, n, of the two branches n'' is the outer deeper head and n' the supernumerary inner and superficial head attached to the external *fabella*. This *fabella* (4) appears as a "Knotenpunkt" of tendon of *M. gastrocnemius* k ($5=\delta$) of the short external lateral ligament (d), and its posterior face is shown by the removal of *M. gastrocnemius* (k) and *M. plantaris* (l).

Plate V, Fig. 10. Left knee-joint seen in posterior aspect. We see the ossicle exposed with its upper inner and outer surfaces, the head of origin of *M. gastrocnemius* being cut through and drawn back over the ossicle (4). We see the ossicle attached to the *ligamentum popliteum* (b) and the short external lateral ligament (d). The position of the sesamoid and its shape are unusual for a *fabella*. It appears to be low down on the external face of the lateral condyle, and approaching the popliteal sulcus. Its position seems at least transitional from that of *fabella* to that of *cyamella*.

Fig. 11. Right knee-joint in posterior aspect. The *fabella lateralis* (4) is seen wedged in so to speak between *gastrocnemius* (k) and *plantaris* (l). This is the position given for it by Cheselden in 1733, and more fully recognised by Sömmering in 1841: see our pp. 18 and 19.

Fig. 12. Left knee-joint in posterior aspect. The *fabella lateralis* (4) has been freed from *gastrocnemius* (k) and seen in relation to the *ligamentum popliteum* (b), the short external lateral ligament (d), and by the opened knee-capsule (a) in relation to its position on the external condylar surface.

It will be seen how great an advance Gruber made in our knowledge of the muscular and ligamental attachments of the *fabellae*.

Fig. 13. Sesamoid of the external condyle in the case of the Wombat (after Pfitzner). This sesamoid rests on the head of the fibula, and appears to be directly associated with the *parafibula* of other Australian types, and again the direct articulation of fibula with the external condyle in other species. These points are discussed in Part II of the present memoir.

Plate VI. Drawings of an actual case of the *fabella lateralis* in man from a cadaver in the Dissecting-Room at University College.

Fig. 14 is a sagittal section of the left femur showing the position of the *fabella* before *M. gastrocnemius* was turned back. Fig. 15 shows the *fabella* in the tendon of the muscle after it has been turned back and the facette on the articular surface of the condyle in which it rested. The closeness of contact differs considerably from the usual position as indicated in the skiagrams: see Plates VII—IX.

Plate VII, Fig. 16 and Fig. 17. Lateral *fabellae.*

Plate VIII, Fig. 18 and Fig. 19. Lateral *fabellae.*

Plate IX, Fig. 20. Small lateral *fabella.* Fig. 21, Large lateral *fabella*, probably differing from the previous illustrations in resting in a facette on the articular surface of condyle. Cf. Plate VII.

Plate X. Most probably a lateral *cyamella* in the neighbourhood of the popliteal sulcus in posterior (Fig. 22) and anterior (Fig. 23) aspects. Is there evidence of a mesial *cyamella*?

Plate XI. There is some evidence in favour of a mesial *cyamella* placed in the groove on the internal epicondyle in Fig. 24. Fig. 25 gives a fair example of a lateral *cyamella* in the popliteal sulcus.

Plate XII, Fig. 26. There is a small bone in the semi-lunar, which may be a posterior lateral *lunula*. Fig. 27 gives more definite evidence of an anterior lateral *lunula*. Both of these *lunulae* are fairly smoothly shaped and do not resemble pathological ossifications: at the same time the damaged condition of lateral condyle in Fig. 26 prevents any stress being laid on the former case. In Fig. 27 there appears to be a well shaped sesamoid at the head of the fibula in close proximity to the *lunula*.

Plate XIII, Fig. 28. This must be taken in conjunction with Plate XIV, Fig. 30. In both cases we have an ossification of the tendon of the quadriceps extensor muscle. In both cases it *may* be considered as pathological, but at the same time its general resemblance to the double or "tandem" *patella*, which occurs regularly in the hare, should be noted. The cases of double *patella* recorded by Gruber (*Virchow's Archiv*, Bd. XCIV, S. 358, 1883) and Wright (*Journal of Anatomy and Physiology*, Vol. XXXVIII. p. 65, 1904) are comparable with each other, but not atavistic in character like those of our skiagrams *. Both our Figs. 28 and 30, seem to suggest the existence of posterior *lunulae*.

Plate XIII, Fig. 29 shows two sesamoids on the face of the lateral epicondyle, possibly related to the lateral femoro-fibular ligament.

Plate XIV, Fig. 31 gives an indication of a single sesamoid in much the same position.

Plate XV, Fig. 32. Lateral *fabella*.

Fig. 33. Lateral *fabella* with a faint trace of a second sesamoid a little below it—possibly but improbably a hemisesamoid of the mesial condyle.

Plate XVI, Fig. 34. Lateral *fabella*. This knee-joint exhibits considerable pathological ossification of the semilunar cartilage.

Fig. 35. Lateral *fabella*.

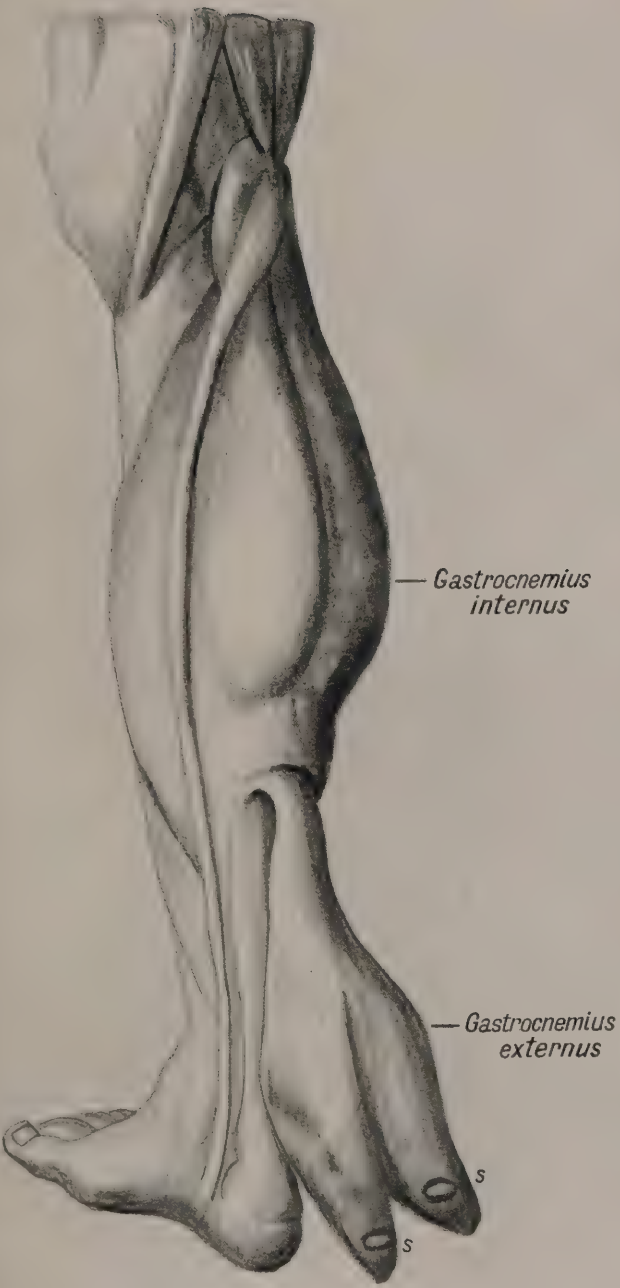
Figs. 32—35 are from skiagrams taken by Dr Melville at the Orthopaedic Military Hospital, and are reproduced from the *Monograph on the Longbones of the English Skeleton*, by Pearson and Bell, Atlas II, CI A and CI B.

Plates XVII and XVIII. Sections of the sesamoids in Foetal Forms. These confirm Gruber's view that a hyaline *cartilago* is the necessary precursor of a sesamoid. Neither hemisesamoid nor orthosesamoid appears to arise from fibrous cartilage. Fig. 36. Section of lateral *fabella* of newly-born kitten, (i) Magnification 45·5, (ii) Magnification 300; showing hyaline cartilage area (*dad*) bordered by fibro-cartilage (*dcd*). Fig. 37. Section of the *cyamella* of a newly-born kitten, (i) Magnification 45·5, (ii) Magnification 300; *a—bb* hyaline cartilage; *bb—cc* intermediate area showing typical rounded nuclei of hyaline cartilage and elongated spindle nuclei of fibro-cartilage, but no threadlike nuclei of fibrocytes; *dd—e* fibro-cartilage showing spindle nuclei and threadlike nuclei. Fig. 38. Longitudinal section of metatarsial sesamoid of full-term human foetus, (i) Magnification 45·5, (ii) Magnification 300, see our p. 27. The metatarsial sesamoid has clearly a hyaline *cartilago* as precursor. Fig. 39. Longitudinal section of *patella* of full-term human foetus, (i) Magnification 45·5, (ii) Magnification 300, see our p. 27. The precursor of the *patella* in man is clearly hyaline.

---

* Tillmans and Bernays had found hemisesamoidal supernumerary *patellae* in cadavers (*Morphologisches Jahrbuch*, IV. Supplement, 1878, S. 442). Presumably these double *patellae* were arranged tandem fashion for Bernays refers to those in cats, mice, and rabbits as similar.

Plate I



ig. 1. First attempt at illustration of the *fabellae* in the two heads of *gastrocnemius*. From Casserius' *Tabulae anatomicae*, 1632.

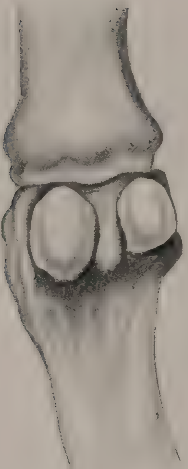


Fig. 2. (c. nat. size.) Sesamoids of first metatarsal of foot in man. Sesamoids known to the Greeks. After Pfitzner.

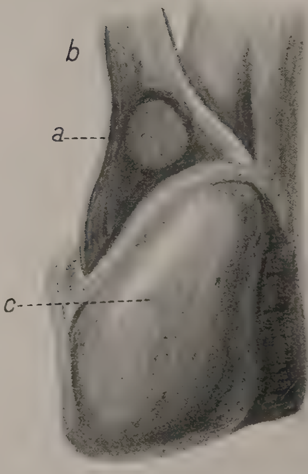


Fig. 3. *Fabella lateralis* as figured by Gillette, 1872. See description of plates.

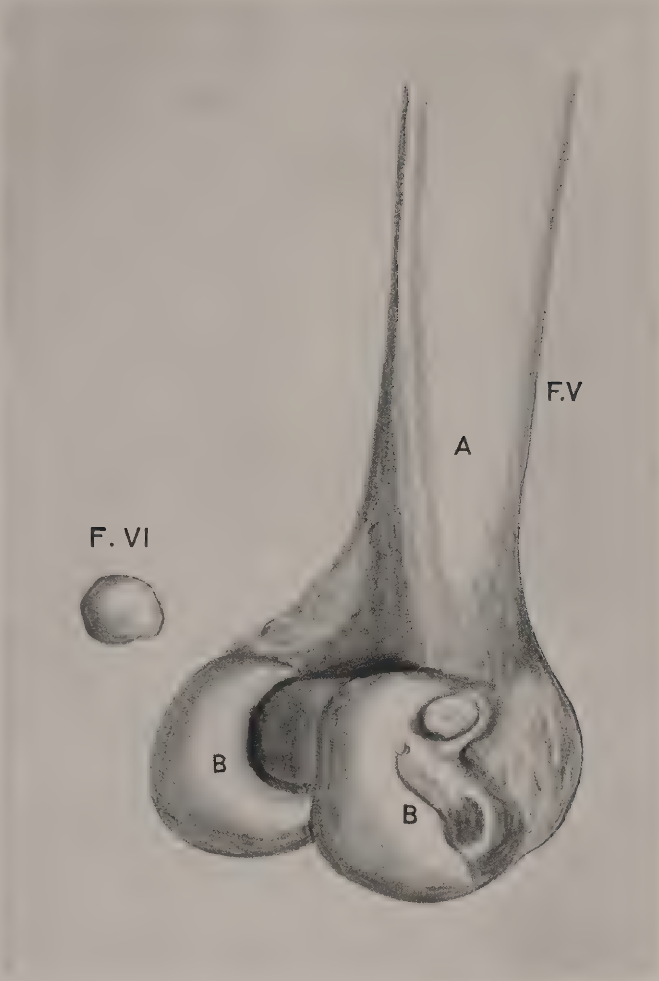


Fig. 4. Trew's rediscovery of the *fabella lateralis*, 1715. Note the unusual position given to sesamoid *C*. (The letter *C* should have been inserted above right hand *B*.)

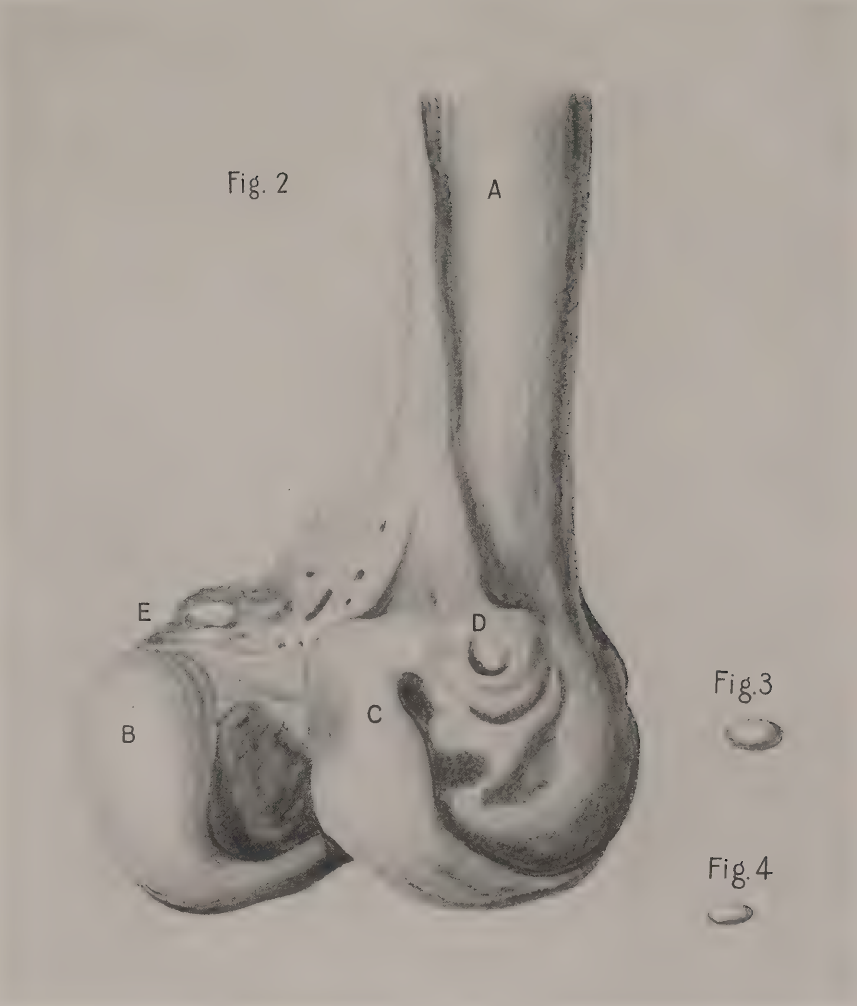


Fig. 5. Heister's "improvement" on Trew; he provided a small *fabella mesialis* in 1732. Both his sesamoids are in very unusual if not impossible places. See description of plates.

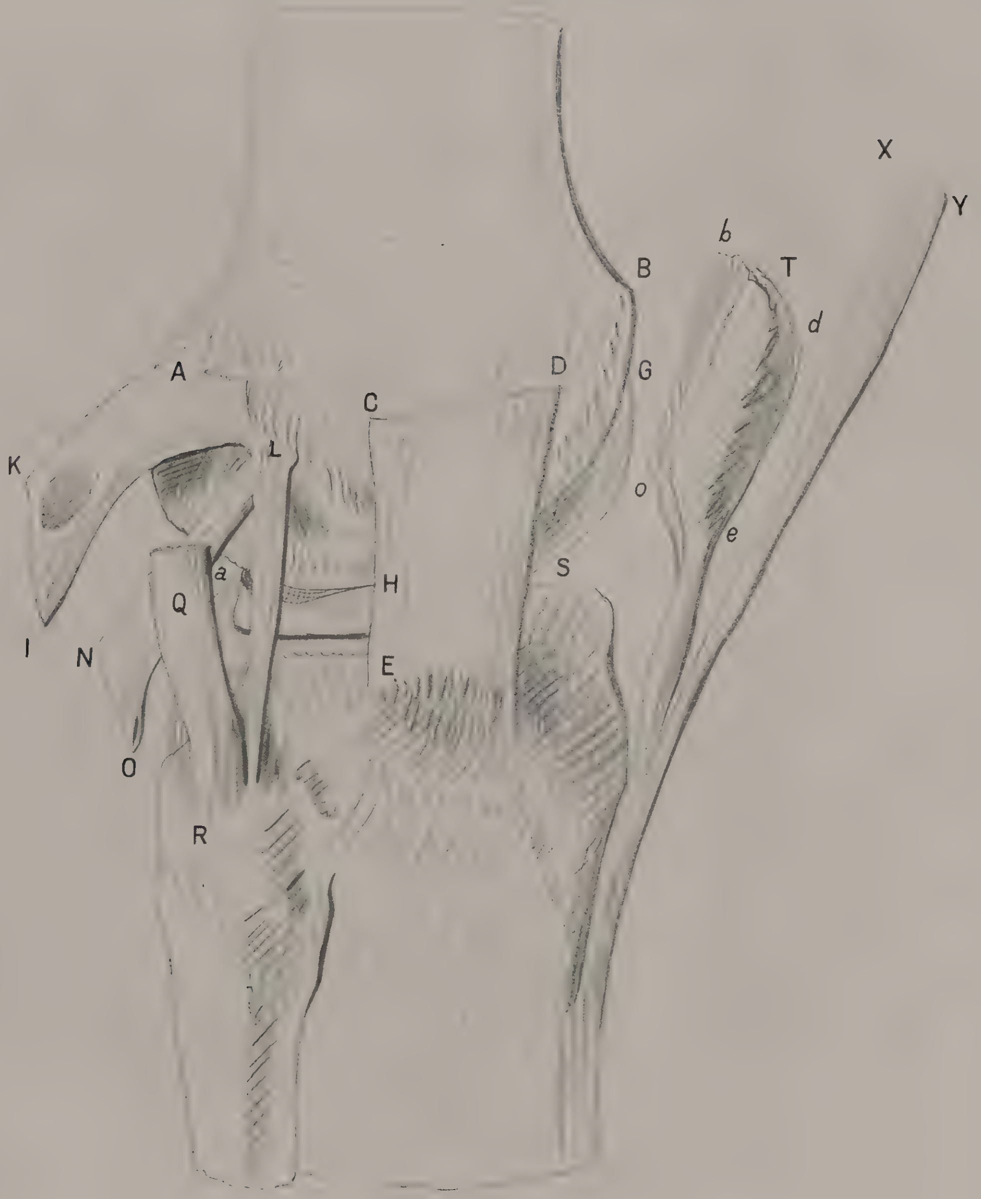


Fig 6. (c. nat. size.) Peter Camper's illustration of the external *fabella* (near *K*) in the tendon of *gastrocnemius*, 1754.

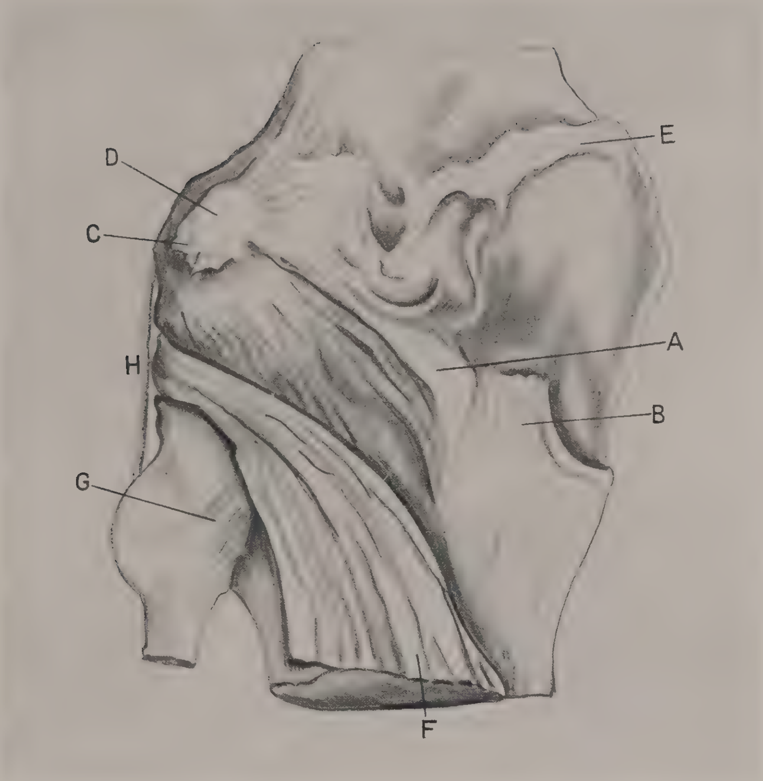


Fig. 7. (c. $\frac{4}{5}$ nat. size.) Sir George Humphry's illustration of the *fabella lateralis.* The sesamoid in correct position, 1858. See description of plates.

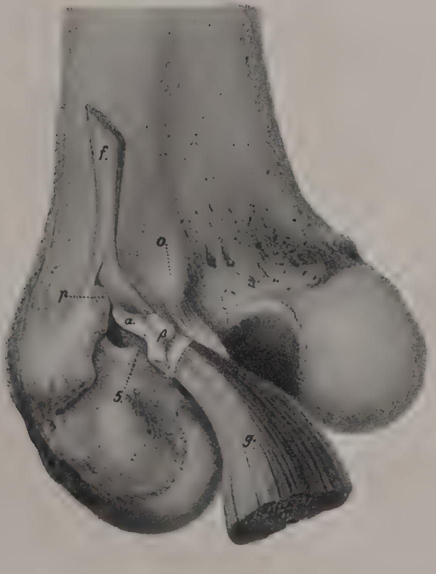


Fig. 8. (c. $\frac{1}{2}$ nat. size.) Pathological ossification at head of internal *gastrocnemius*, Gruber, 1876.

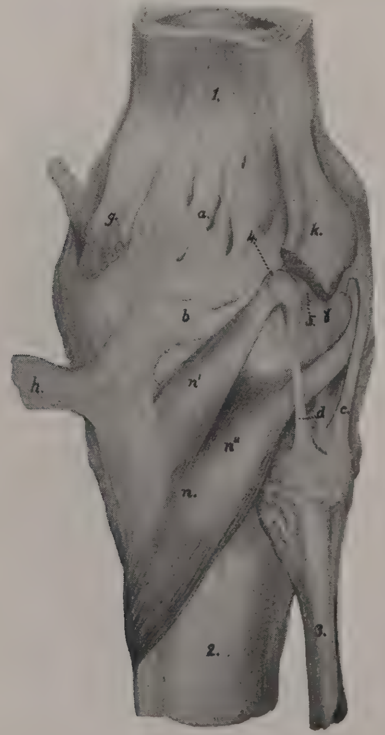


Fig. 9. (c. $\frac{1}{2}$ nat. size.) *M. popliteus biceps*, the additional head as well as the *ligamentum posticum* and *M. gastrocnemius* joining the *fabella lateralis*, Gruber, 1876.

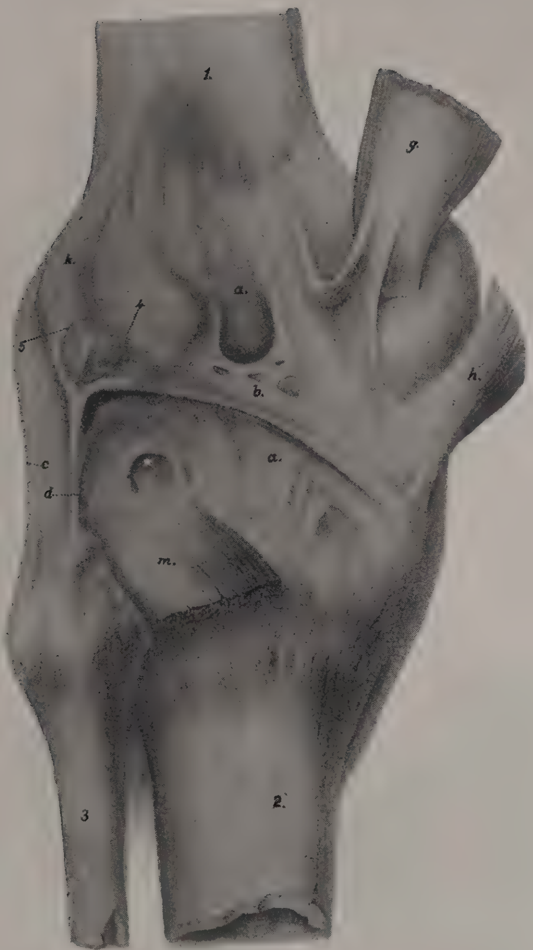


Fig. 10. (c. $\frac{5}{8}$ nat. size.) Ossicle (4) at "Knotenpunkt" of *M. gastrocnemius* (*n*). *Ligamentum popliteum* (*b*), and *Ligamentum posticum* (*d*), Gruber, 1876.

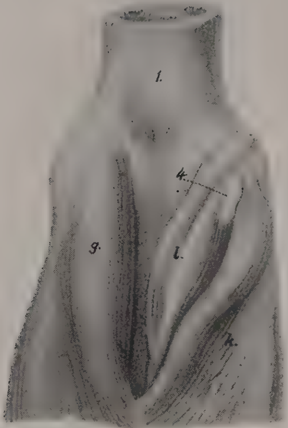


Fig. 11. (c. $\frac{3}{8}$ nat. size.) External *fabella* (4) in relation to *M. gastrocnemius* (*k*), and *M. plantaris* (*l*), Gruber, 1876.

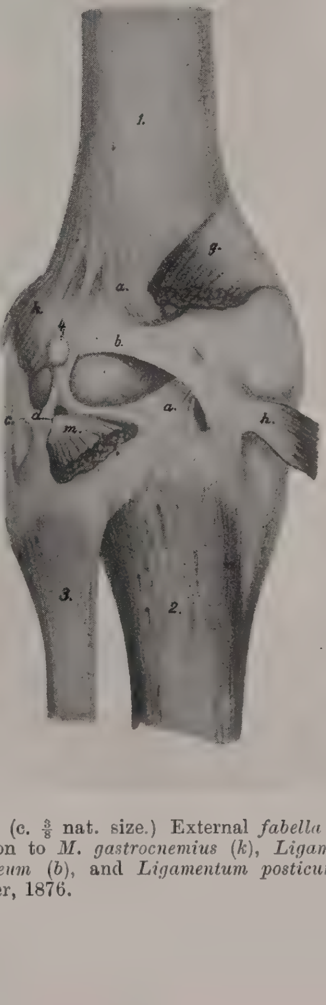


Fig. 12. (c. $\frac{3}{8}$ nat. size.) External *fabella* (4) in relation to *M. gastrocnemius* (*k*), *Ligamentum popliteum* (*b*), and *Ligamentum posticum* (*d*), Gruber, 1876.

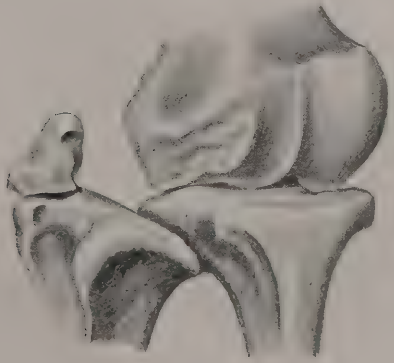


Fig. 13. (c. nat. size.) Sesamoid on the head of the fibula in the case of the Wombat, Pfitzner, 1892. See description of plates.

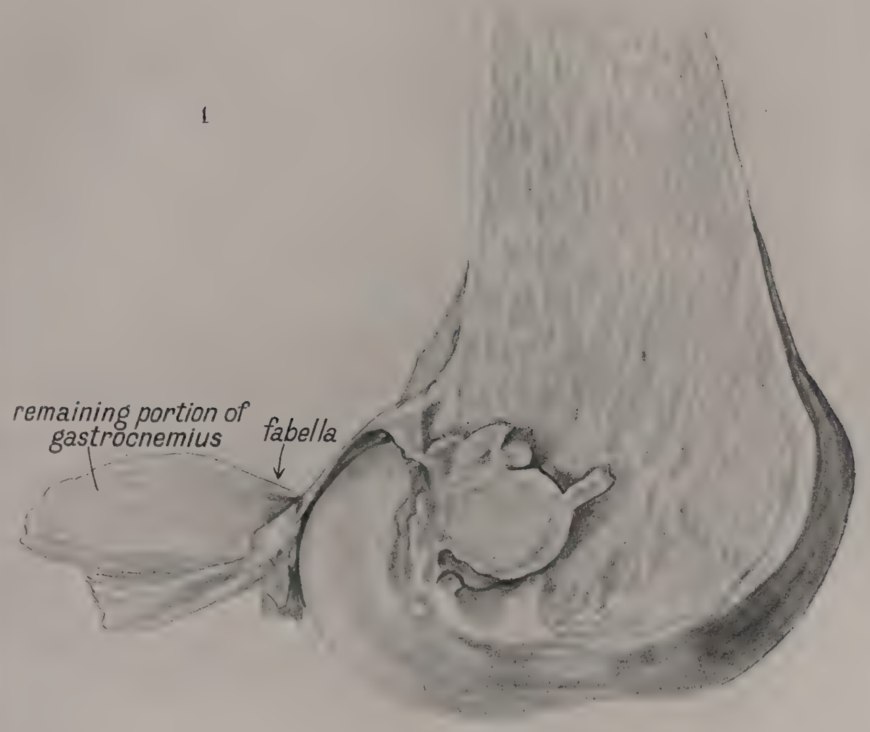


Fig. 14.

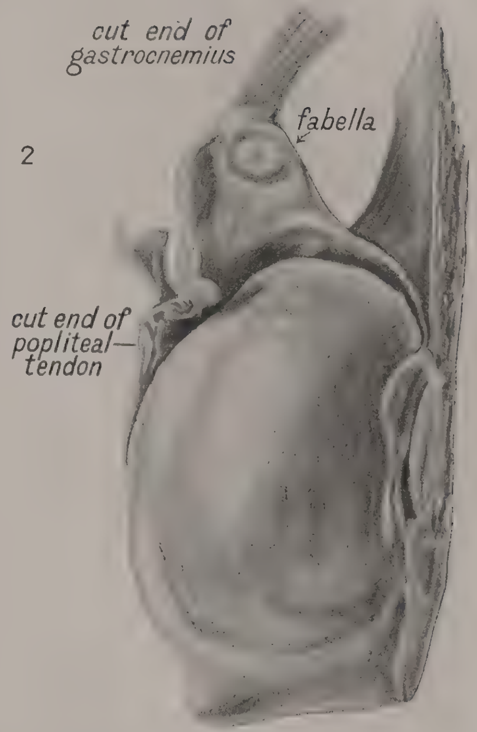


Fig. 15.

Drawings illustrating the position of the external *fabella* in man from a case occurring in the Dissecting-Room at University College, 1919. This is a relatively rare position: compare the skiagrams of the knee-joint. See description of plates. Circa $\frac{5}{4}$ nat. size.

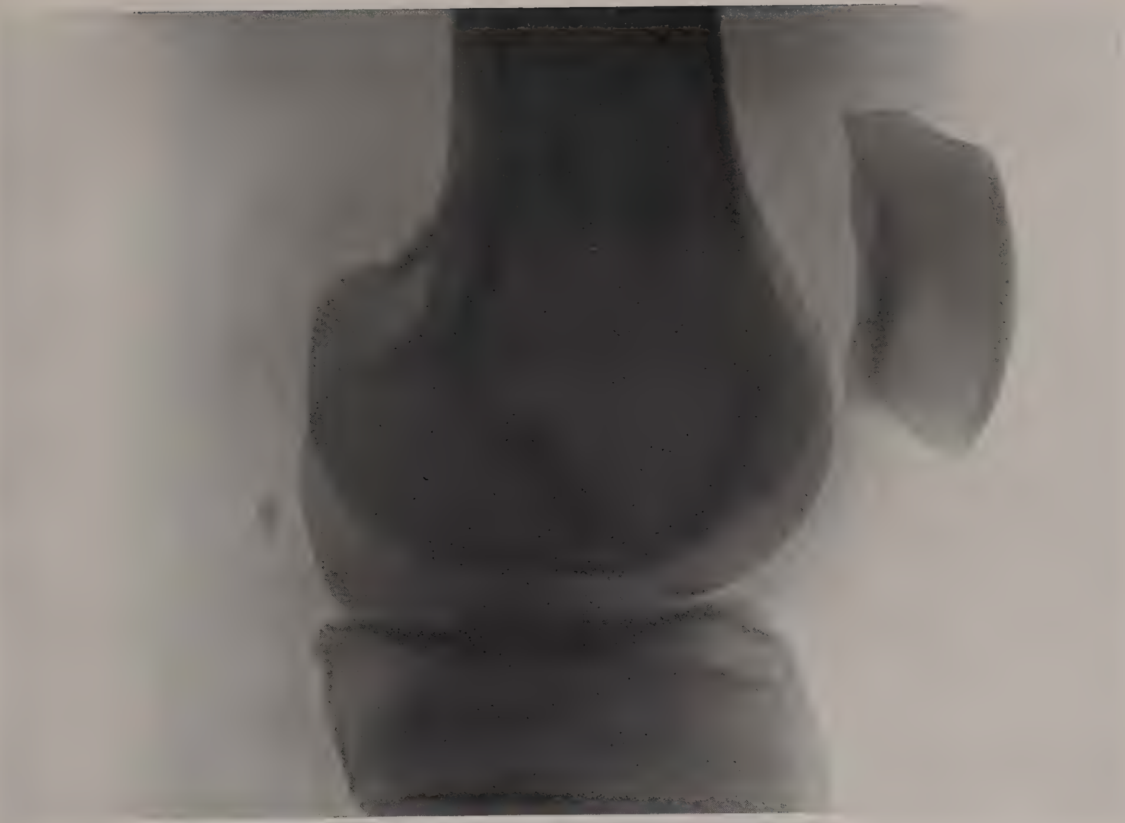


Fig. 16. Small lateral *fabella*.

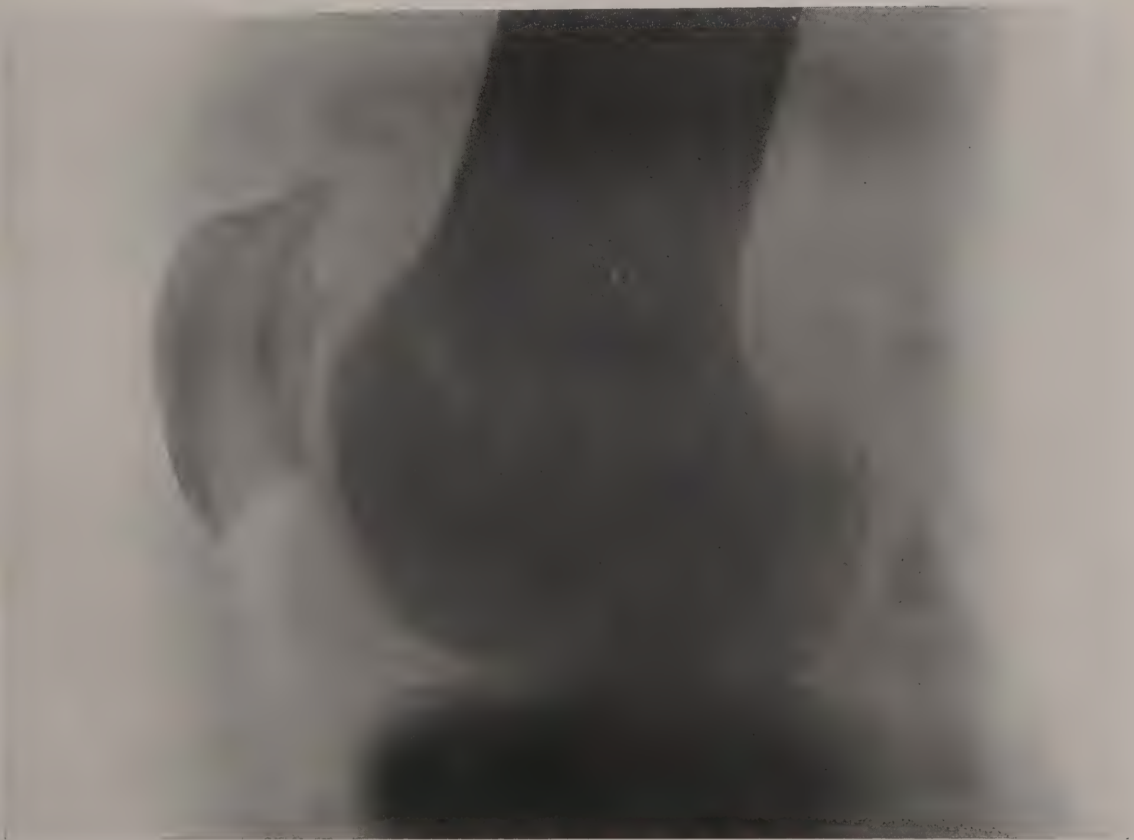


Fig. 17. Large lateral *fabella*.

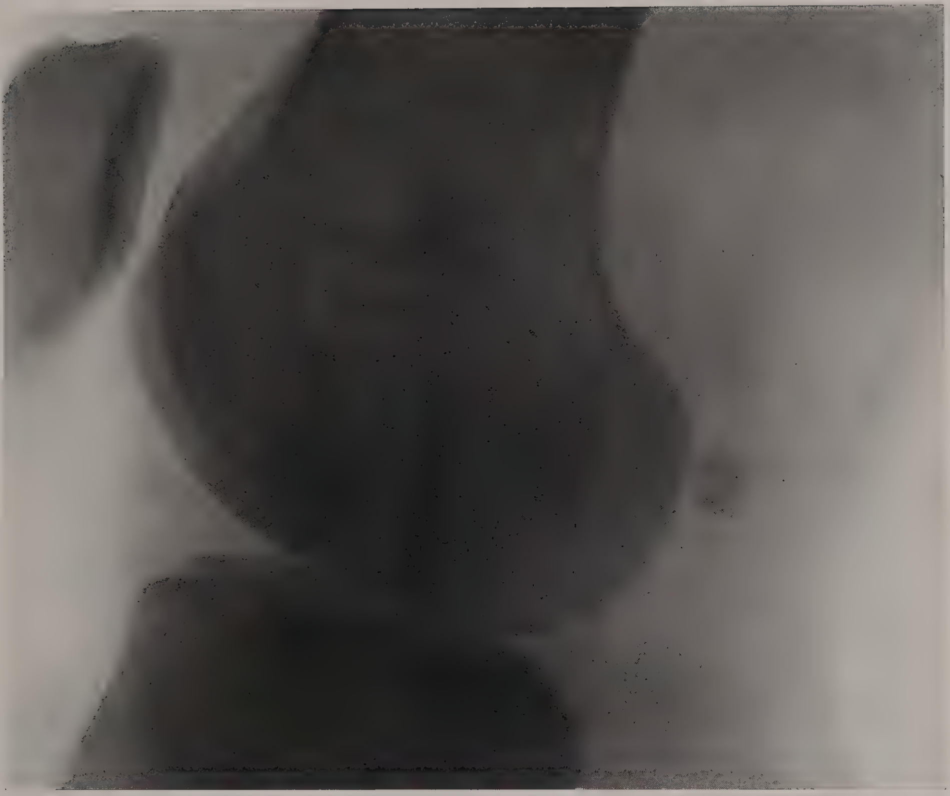


Fig. 18. Large lateral *fabella*.

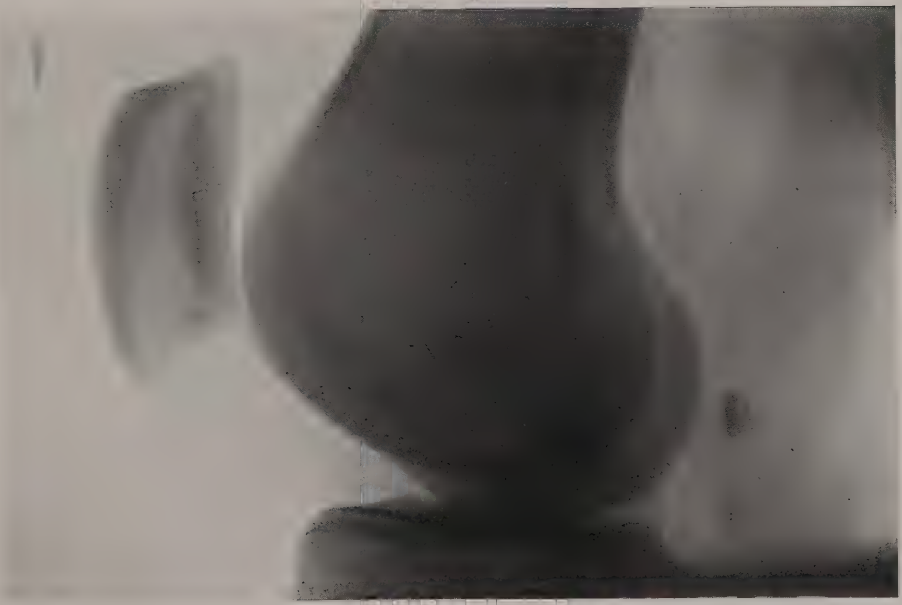


Fig. 19. Lateral *fabella*.

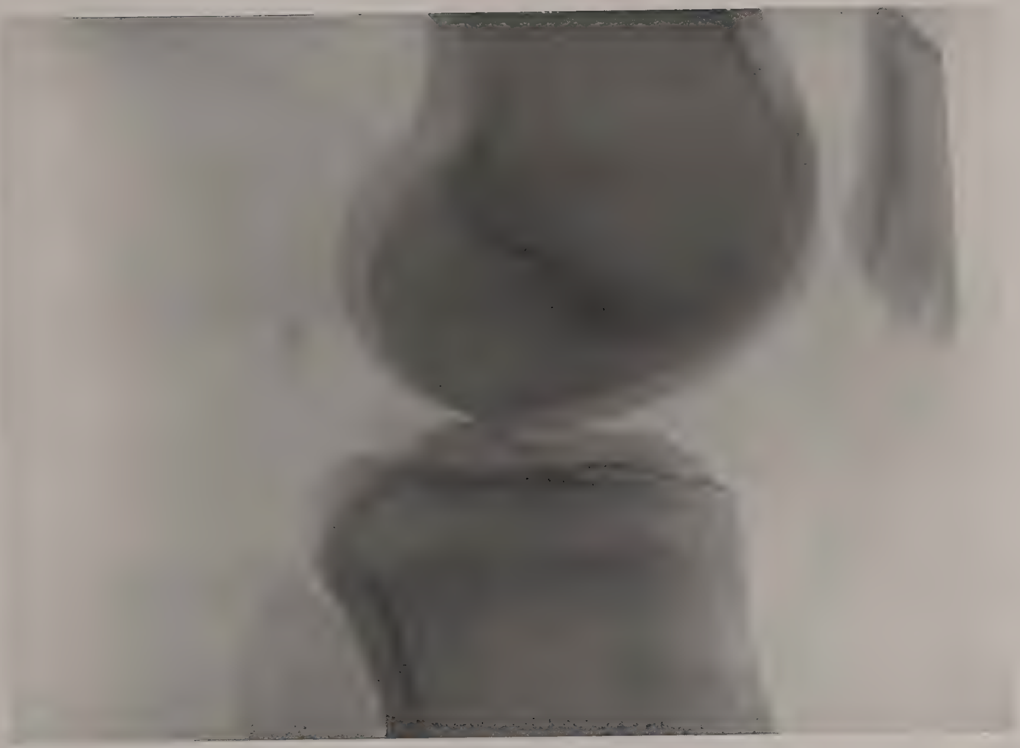


Fig. 20. Small lateral *fabella*.

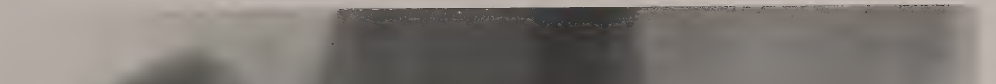


Fig. 21. Large lateral *fabella*.

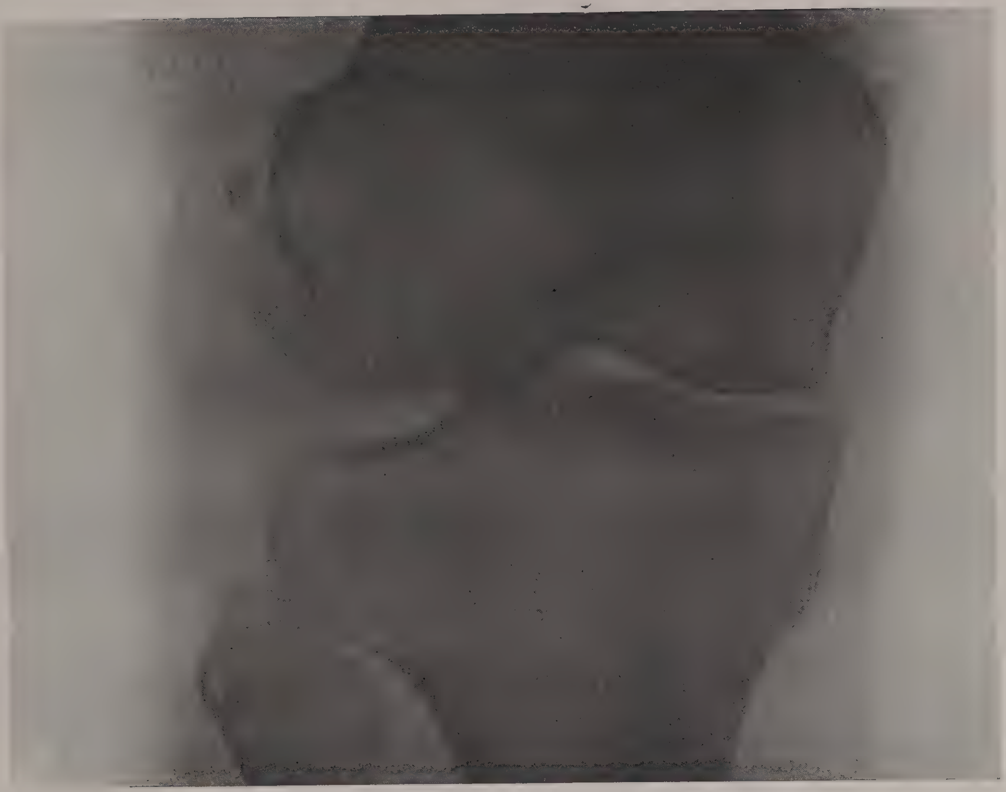


Fig. 22. Lateral *cyamella* in popliteal sulcus in posterior aspect.

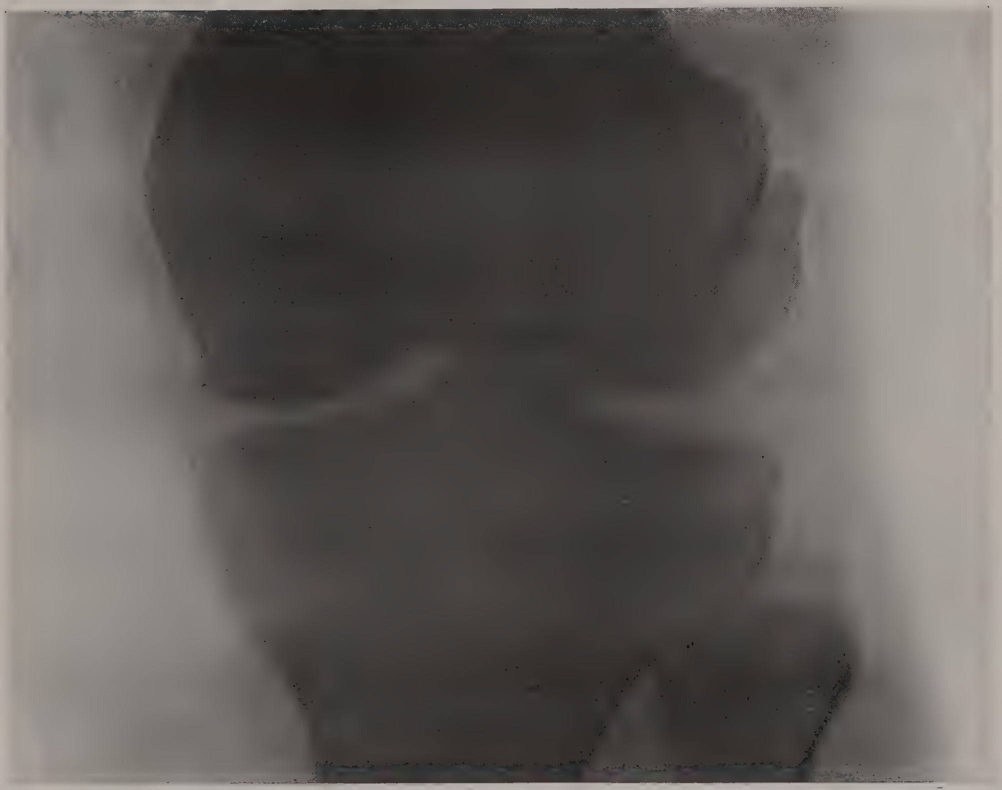


Fig. 23. The same sesamoid in anterior aspect.
Note in both figures the possibility of a mesial *cyamella*.

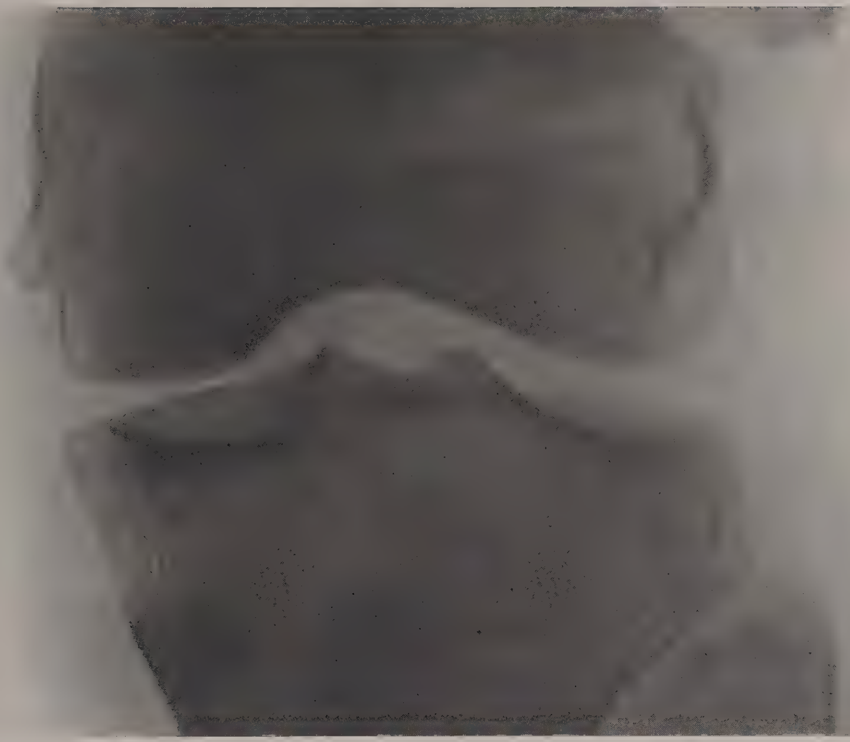


Fig. 24. Occurrence of what might possibly be interpreted as a mesial *cyamella*.

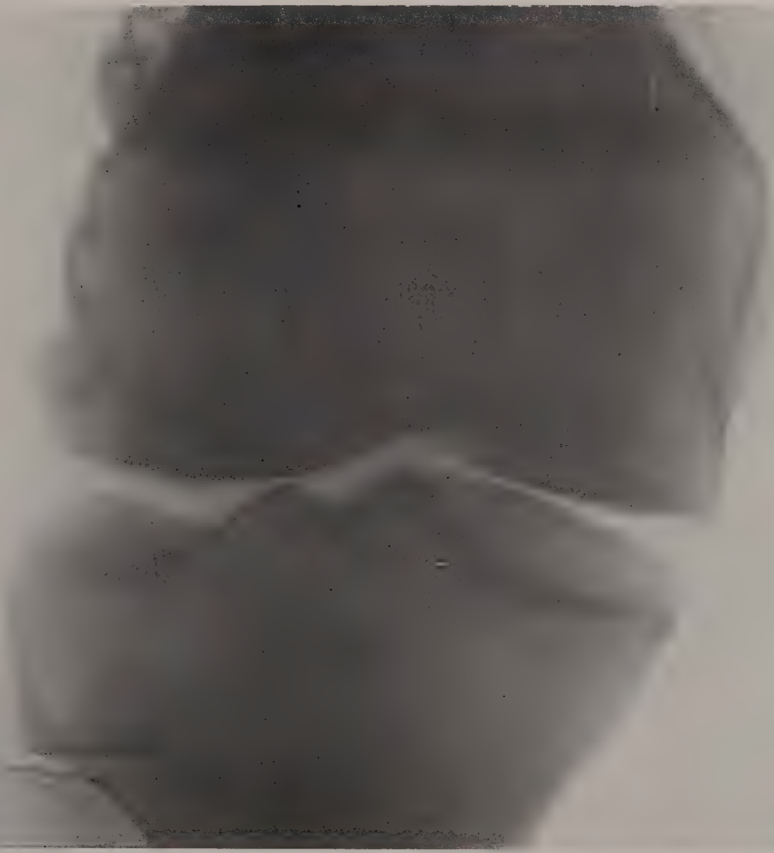


Fig. 25. Lateral *cyamella* in popliteal sulcus.

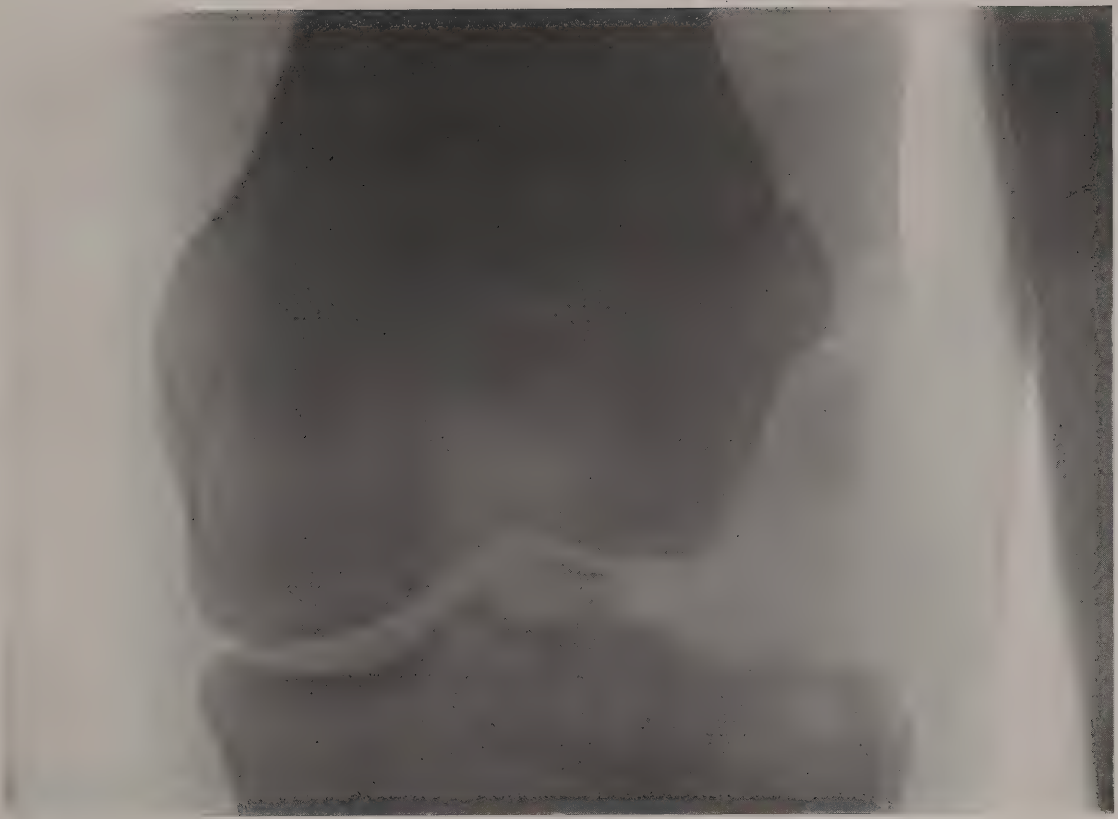


Fig. 26. Lateral *lunula.*

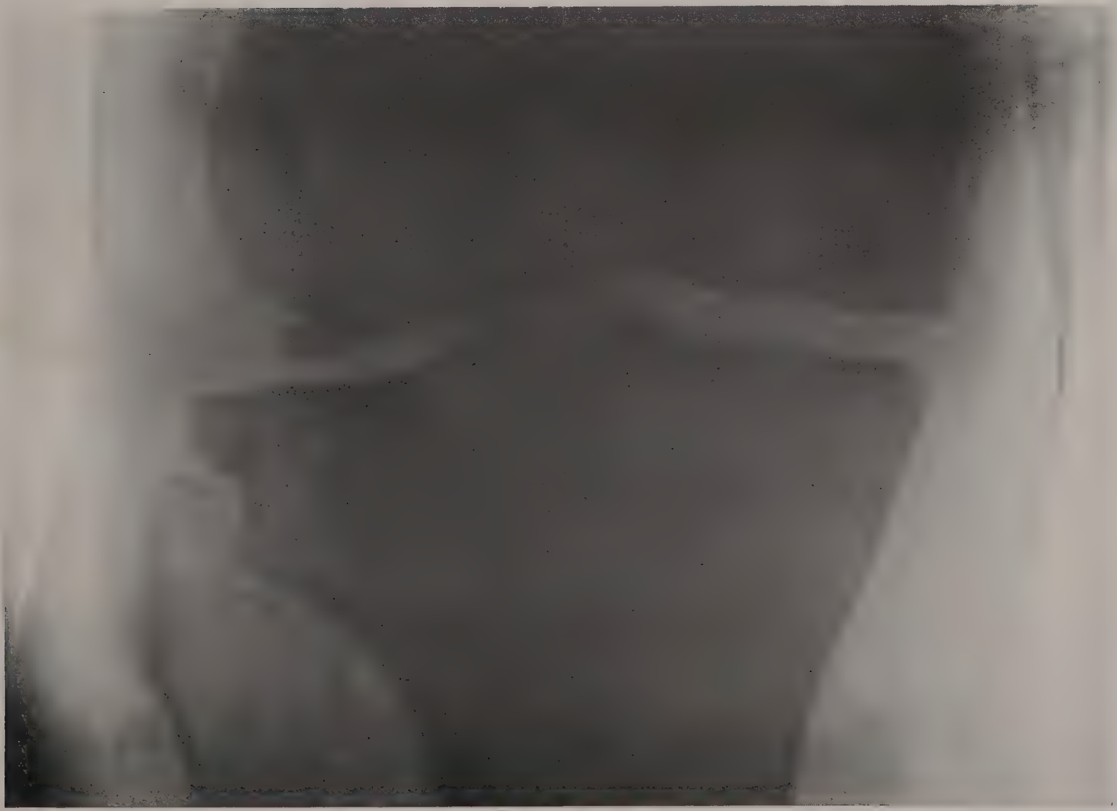


Fig. 27. Another case of lateral *lunula.* Also a sesamoid above the head of the fibula (? displaced *fabella*).

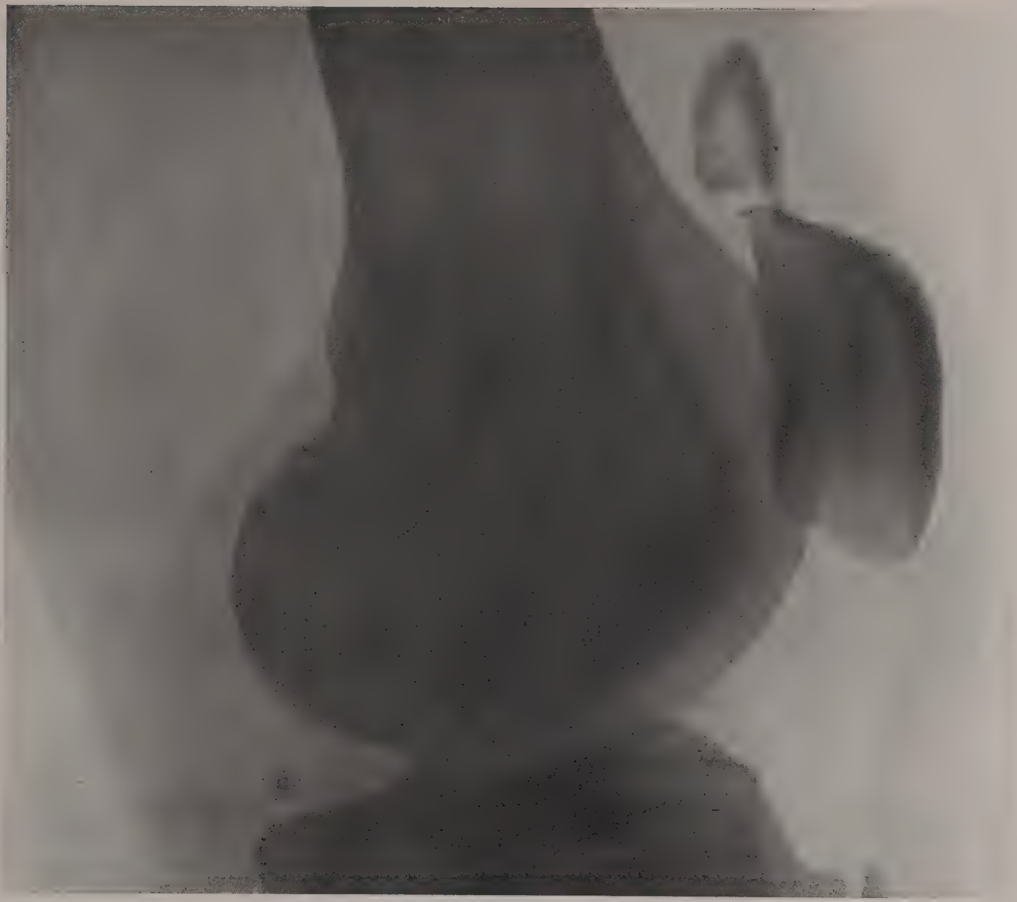


Fig. 28. Double *patella* and posterior *lunula* (?).

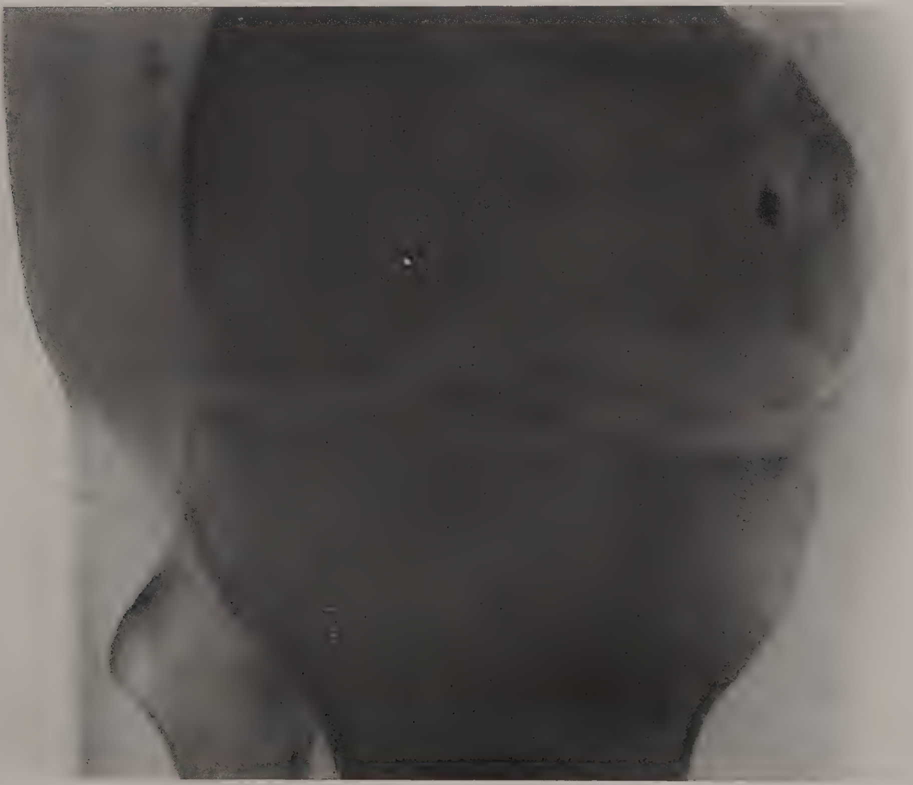


Fig. 29. Two small lateral sesamoids in unusual positions, possibly associated with the lateral femoro-fibular ligament.

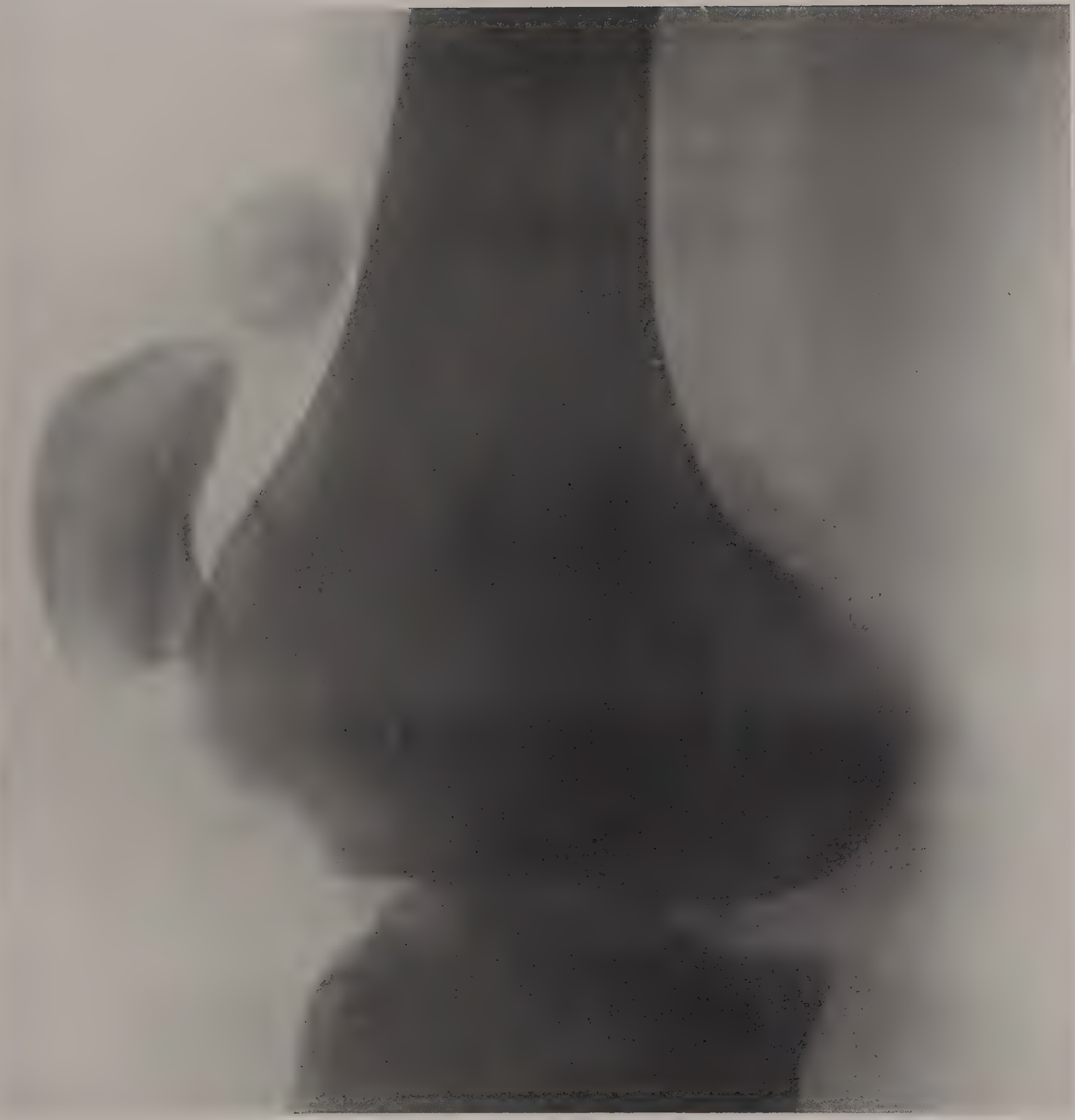


Fig. 30. Double *patella*. (? Small external posterior *lunula*.)

Fig. 31. Sesamoid in femoro-fibular ligament? Cf. Plate XIII, Fig. 29.

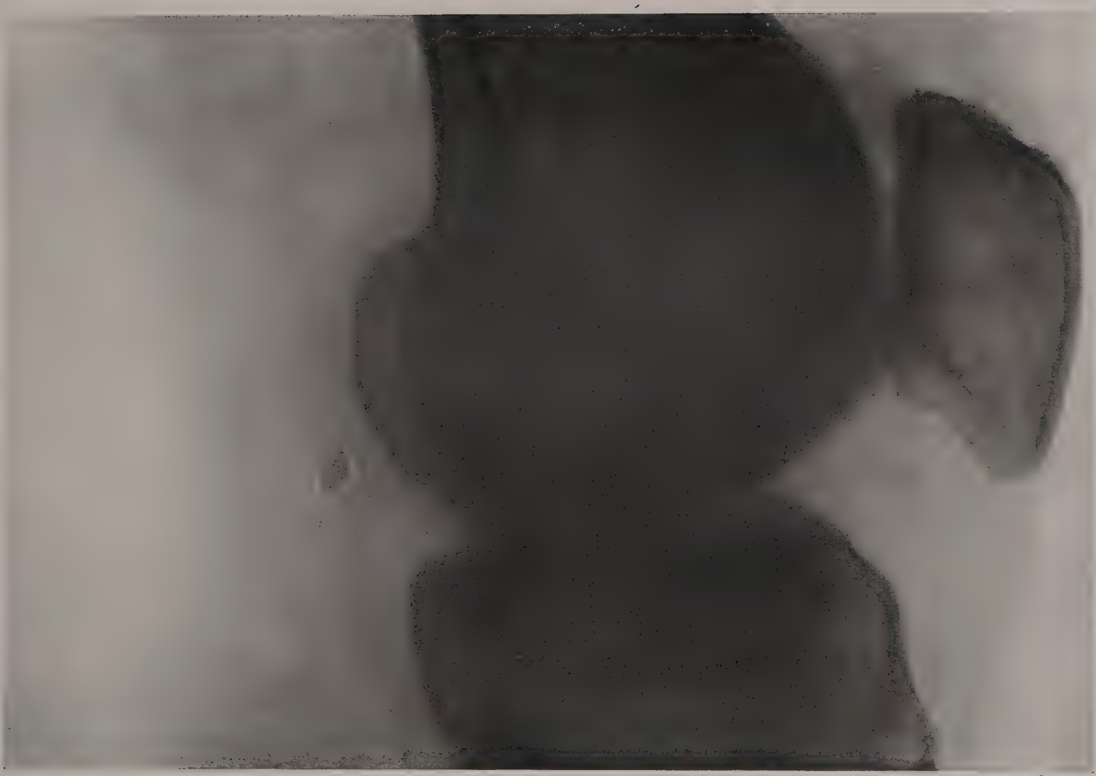


Fig. 32. Lateral *fabella*.

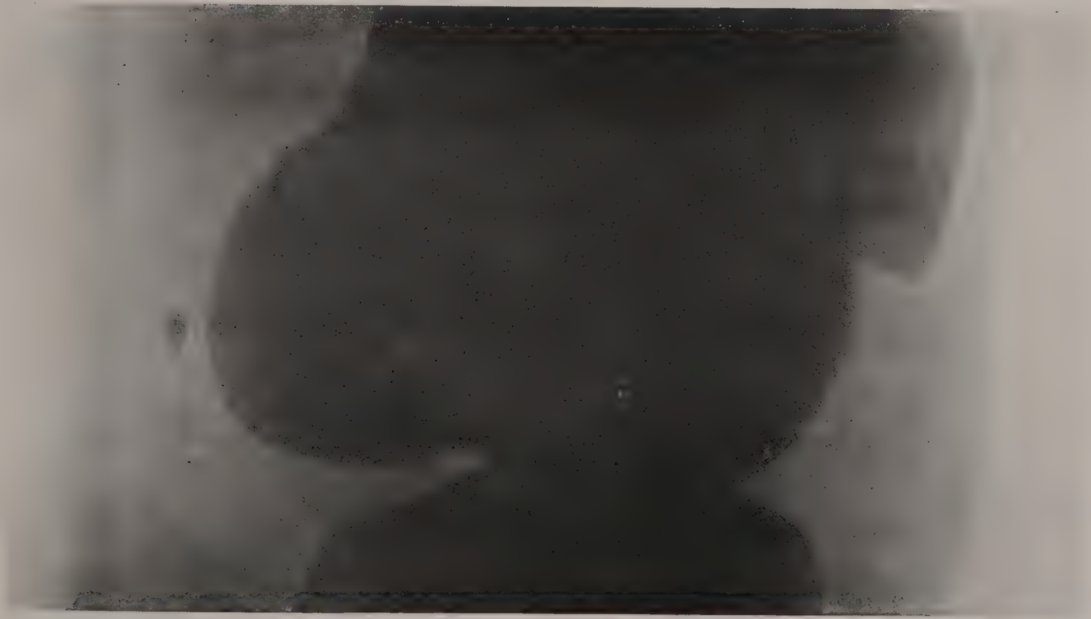


Fig. 33. Lateral *fabella*, with some trace of a second sesamoid beneath it.

Figs. 32 and 33 are reproduced from Atlas, Part II, to the *Monograph on The Long Bones of the English Skeleton*, by Pearson and Bell.

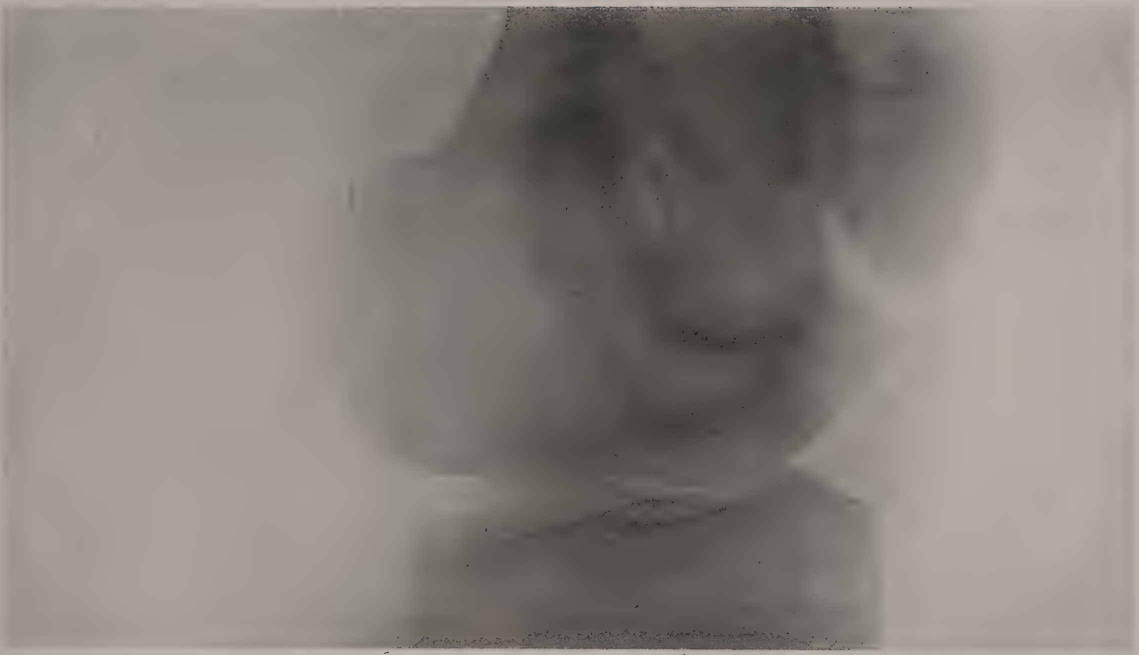


Fig. 34. Lateral *fabella*.

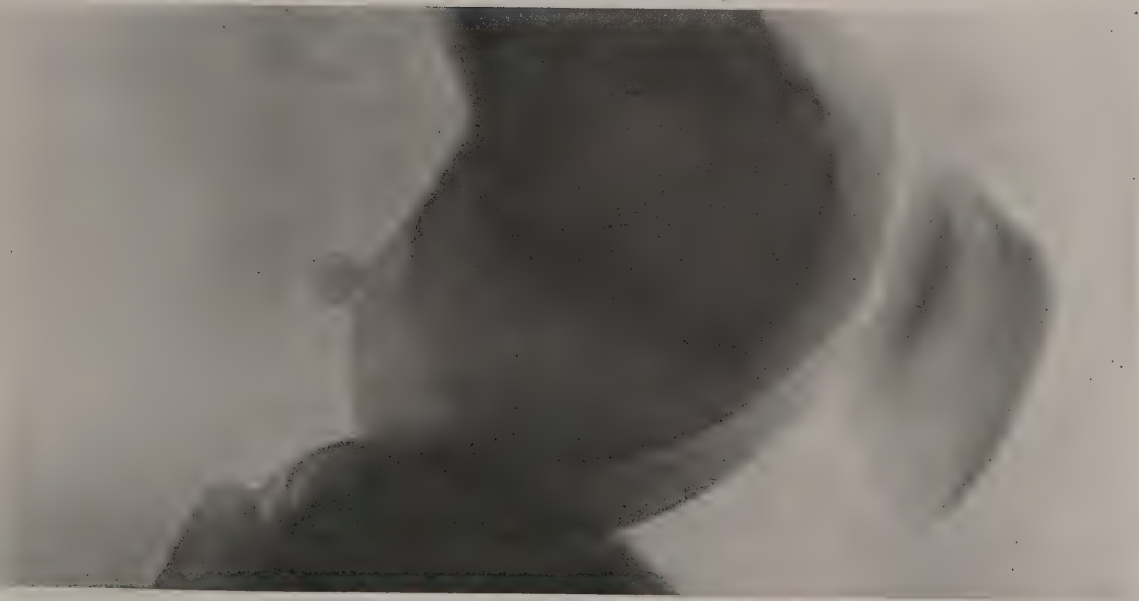
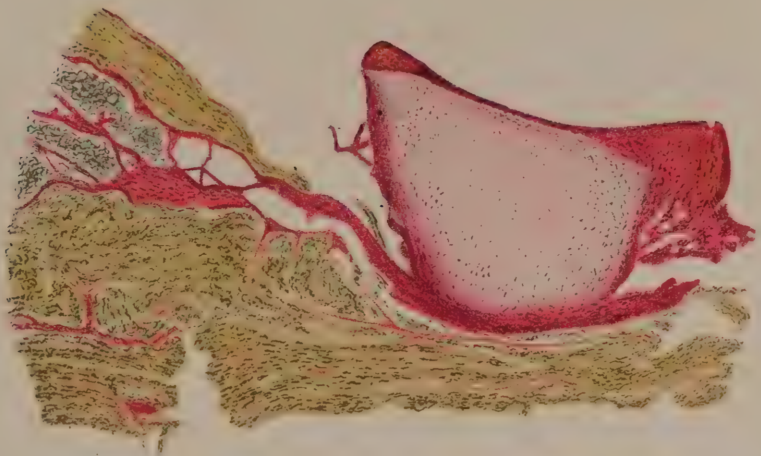


Fig. 35. Lateral *fabella*.

Figs. 34, 35 are reproduced from Atlas, Part II, to the *Monograph on The Long Bones of the English Skeleton*, by Pearson and Bell.

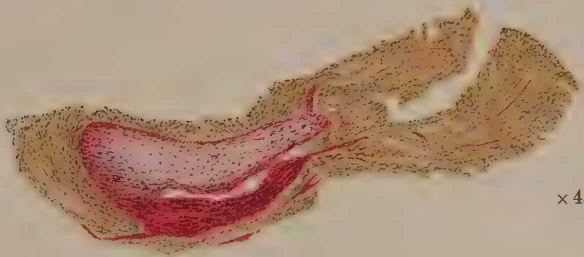
Plate XVII

Fig. 36 (i).

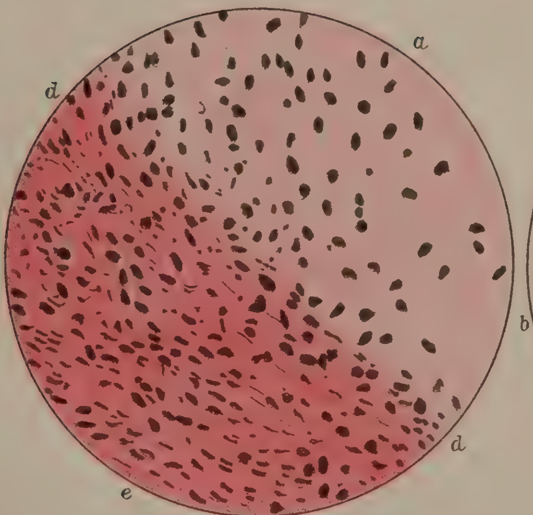


× 45·5

Fig. 37 (i).

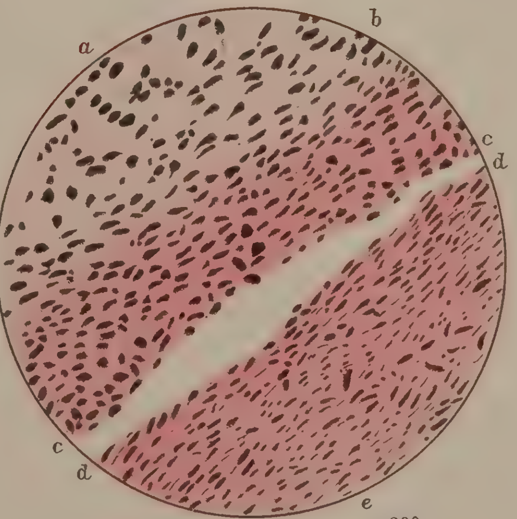


× 45·5



× 300

Fig. 36 (ii).



× 300

Fig. 37 (ii).

Sections of the Sesamoids of a Newly-born Kitten.

Plate XVIII

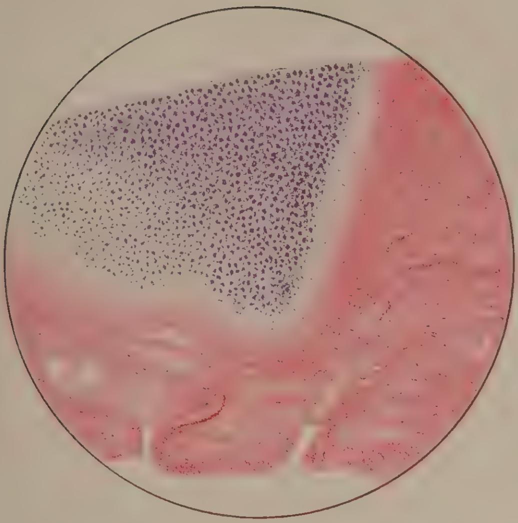


Fig. 38 (i). × 45·5

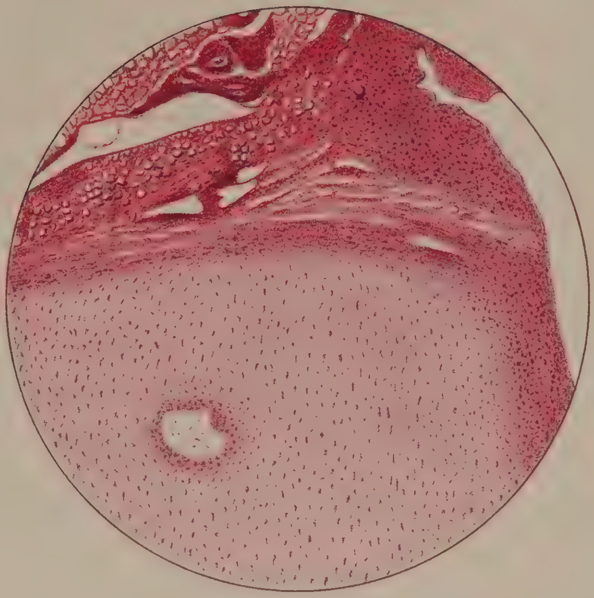


Fig. 39 (i). × 45·5

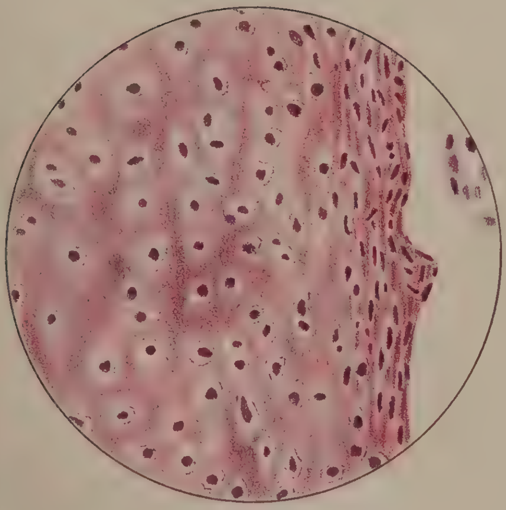


Fig. 38 (ii). × 300

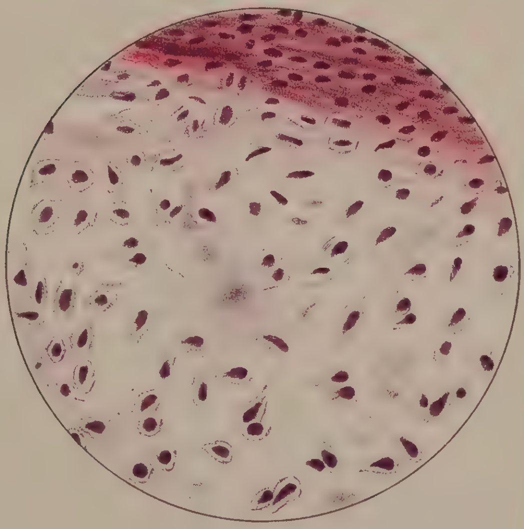


Fig. 39 (ii). × 300

Sections of the Sesamoids of a full-term Human Foetus.

PART II

EVOLUTION OF THE SESAMOIDS

ON THE SESAMOIDS OF THE KNEE-JOINT.

By KARL PEARSON, F.R.S. and ADELAIDE G. DAVIN, B.Sc.

PART II. EVOLUTION OF THE SESAMOIDS.

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(8) *Further Remarks on Origin of Sesamoids.*

In the first part of this paper attention was drawn to Gruber's statement that the sesamoid invariably arises from hyaline cartilage. We cited our own work as supporting this view and a considerable number of further sections made since entirely confirm it. We do not think it needful to publish the drawings made from these sections—they all show the same hyaline structure; and we now hold with Gruber that no thickening in the tendons of *M. gastrocnemius* or *M. popliteus* should be classed as a hemisesamoid unless it shows this hyaline structure*. Every orthosesamoid will be found to exhibit this prefiguration if the knee-joint be examined in the embryonic or early post-natal states.

---

* Another matter of some interest is elucidated by our sections. Lunghetti (*Internationale Monatschrift für Anatomie und Physiologie*, Bd. xvi. § 47) following Gillette in his classification of sesamoids into peri-articular and intratendinous claims to have shown that the origin of the peri-articular sesamoids is totally different from that of the intratendinous. We have already (p. 24) criticised Gillette's classification; it does not seem to us in accordance with the evolutionary origin of the *fabella lateralis* and the *cyamella*, both are ultimately peri-articular in origin, and our sections seem to show that Lunghetti's view is erroneous. He asserts that the peri-articular are prefigured by hyaline cartilage which can be noticed in the foetus with the form of the definite bone. With this we are in agreement; the sections of the metatarsal sesamoid in the human foetus (p. 27) demonstrate it. Lunghetti further asserts that the intratendinous only appear in the adult in the middle of a fibrous tissue which chondrifies a short time before ossification. This assertion may be true of pseudo-sesamoids such as the osteomata of riders. It is entirely erroneous in the case of *fabellae* and *cyamella* which can be detected in embryos and the young shortly after birth by the presence of patches of hyaline cartilage as we have indicated: see our pp. 26—27 and Plates XVII and XVIII.

Two points of much bearing on what follows later were reached as the outcome of these investigations:

(*a*) The *cyamella* of the rabbit was found near the head of the fibula, there was no marked popliteal groove for it to lie in.

(*b*) The lateral and mesial *fabellae* while both prefigured by hyaline cartilage in kittens were very unequal the former being far more developed. Pfitzner* says that he found the *fabella medialis* absent in 29 cases out of 52 in the cat. He states that it always occurs in dog, fox and hare. Meckel† states that both in cat and dog only the external *fabella* occurs. Gruber‡ places *Canis familiaris* (as well as *C. vulpes* and *C. lupus*) and *Felix domesticus* in the group which have both *fabellae*. Thus he tells us that in puppies at birth he found hyaline cartilage and later orthosesamoids; the external ossified first at about six months. The external *fabella* articulated with the femur in a trough ("Grube") with projecting rim on the upper part of the external condyle of the femur; the internal *fabella* was in a less marked trough on the upper part of the internal condyle. With regard to newborn kittens both *fabellae* were prefigured by hyaline cartilages: the external ossified first and the internal was smaller and of a different shape.

(9) *Carnivores.*

While our experience with kittens accords with that of Gruber, and not with that of Pfitzner, and while we have found the two *fabellae* in many adult dogs, we have not invariably found the mesial *fabella* after most careful sectioning of the tendon of the internal head of *gastrocnemius* in puppies of a fortnight old (failed in two cases). On a general balance of the evidence therefore we are inclined to believe that cases do occur in the smaller carnivores, in which both *fabellae* are not present, although Meckel's view that only one occurs in dog, cat and fox is certainly incorrect.

While dealing with the carnivores we may note that Gruber examined a female, aged one year, of *Felis leo*, and found an external hemisesamoid, the internal was represented by a pad ("Wulst") with no cartilage cells (*loc. cit.* p. 59). Further in *Gulo vittalus* there was an external *fabella* only, which as in man did not articulate with the femur, but lay in the tendon of *gastrocnemius*, and between that and the knee capsule (p. 57). Further the external *fabella* and that only has been found by Gruber in *Nasua*, *Ursus arctos*, *Mustela alpina* and *Lutra marina*. Blainville found none in *Ursus*, Meckel found the external only. The latter found the external only in *Felix lynx*, the raccoon, and the hyaena§, while Blainville and Owen found both in the hyaena; and Meckel found both in *Mustela* and *Lutra*. Davis|| and

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* See work cited (*Biometrika*, Vol. XIII. p. 163), S. 582.

† *System der vergleichenden Anatomie*, S. 634, 635, Halle, 1828.

‡ See work cited (*Biometrika*, Vol. XIII. p. 156), pp. 57, 58.

§ *Loc. cit.* S. 634—635.

|| *Journal of Anatomy and Physiology*, 1888, p. 215.

again Young* found the external *fabella* only in *Viverra civetta*†; and Macalister found none in the Laughing Otter (*Aonyx*)‡.

Lack of material has hindered our undertaking a considerable number of independent dissections on the carnivores; we have been largely compelled to examine prepared skeletons, and these can never prove a negative. They may, however, give positive evidence, and often confirm or refute earlier statements. The chief difficulty is one we have already referred to—the articulator preserves the *fabellae*, but far more rarely, when it exists, the *cyamella*.

We have found both *fabellae* and *cyamella* in: *Proteles cristatus* (Aard-Wolf), *Canis vulpes* (fox), *Canis domesticus* (not invariably) and *Felis domestica*§ (invariably: see Plate XX, Fig. 44).

We have found both *fabellae*, no *cyamella* in *Felis catus* (wild cat), the two-spotted Paradoxure, the *Hyaena crocuta* (spotted Hyaena), *Otocyon lalandii* (long-haired fox), the Java otter, *Cryptoprocta ferox* (fossa) where the external was much larger than the internal, *Felis nebulosa* (clouded leopard), *Canis melitus* (American wolf), *Cyon sumatrensis* (Malayan wild dog).

We have found the external *fabella* only in *Lutra canadensis* (Canadian otter), *Aelurus fulgens* (Panda), *Lutra vulgaris* (otter), *Enhydra marina* (sea otter), where the external *fabella* was markedly large and there was a much emphasised excavation corresponding to it above the external condyle on the shaft of the femur itself (see Plate XIX, Fig. 40), *Felis tigris* (2 cases)—*Eupleres goudoti* (a Madagascar

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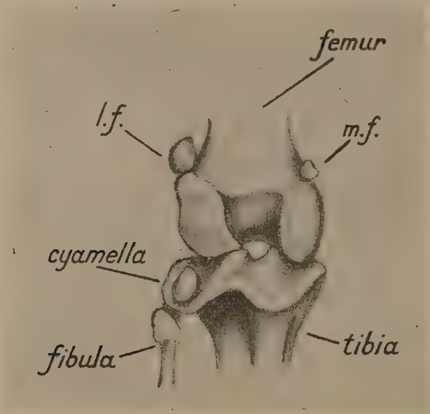
* *Journal of Anatomy and Physiology*, 1879, p. 174.

† Macalister (*Proc. Royal Irish Acad.* Vol. I. 2nd series, p. 512), states that there is a hemisesamoidal *cyamella*.

‡ *Proc. Royal Irish Acad.* Vol. I. *Science*, 2nd Series, p. 545.

§ The cat is a very good example of the complete system in the carnivores (see accompanying drawing after Plate XXV, Fig. 6 of Pfitzner's memoir). In it we see the intimate relation of the *cyamella* to



both head of fibula and head of tibia, with the latter of which it articulates. The close association of external *fabella* with the *cyamella* when the limb is flexed is evident and also the dominance of the former over the mesial *fabella*.

viverrid), cheetah (2 cases), *Herpestes ichneumon* (the Egyptian ichneumon) with both lateral *fabella* and *cyamella*, *Canis dingo**.

We have not been able to confirm Gruber's result for the lion or Meckel's for bears. In *Felis leo* we have found a deep cavity on the articular surface of the external condyle which might well be for an external *fabella*. On a skeleton of *Ursus horribilis* (grizzly bear) we found nothing, but on the fossil *Ursus spelaeus* (great cave bear) there were depressions on the femur which might well have served for *fabellae*. The same remark applies to the fossil *Arctotherium bonariensi*, which we also examined.

We have purposely discussed the carnivores in the first place as a group marked by sesamoidal characters intermediate between the Primates and Ungulates. The higher primates have lost wholly or in part both *fabellae* and *cyamella*; the higher carnivores are in the same stage. Either they have never developed them, or they have lost them and comparison with the primates suggests that the latter is the better account. But one great feature comes out of any examination of the carnivores: There is no single species in which the mesial *fabella* is present without the external. If one *fabella* alone occurs, it is the external. The mesial *fabella* seems to be a pale reflex of the external *fabella*. It is often absent, often much smaller, oftener remains a hemisesamoid, and when it does ossify, ossifies later. Its development in the individual suggests a different evolutionary origin, and one of less importance than that of the external *fabella*.

(10) *Ungulates.*

Let us now pass to the Ungulates and note first what others have observed. Among the true ungulates, the *Perissodactyla*, tapirs, horses, etc., no *fabellae* have been seen. Among the *Artiodactyla* the swine† are without them and nearly all the ruminants. The only exception that we have seen noted is that of the stag, which is said by Meckel to have an external *fabella*. This is supported by Gruber, who says he found the external *fabella* in *Cervus tarandus* but otherwise in none of the ruminants. It fails in other members of the *Ungulata*, horse, elephant, hippopotamus, rhinoceros, giraffe, etc., etc.

While we have found sesamoids preserved in mounted skeletons of nearly all the lower primates, the rodents and certainly fifty per cent. of the carnivores, we have drawn a complete blank with the exception of *Hyrax* in the case of all ungulates. There seems no reason why the articulator should have made a practice of removing the *fabellae* in the case of the ungulates.

We have examined skeletons of: *Ovis aries*‡, *Bos indicus*, *Capra hircus* (common goat), *Capra tartarica* (Saiga antelope, 3 cases), *Tetraceros chiliana* (four horned antelope, 4 cases), *Moschus moschiferus* (musk deer), *Cervus dama* (fallow deer),

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* Only one case, which had solely the external *fabella*. But the dogs are very difficult unless directly dissected. We have noted both *fabellae* in articulated skeletons of Saint Bernard, French Bloodhound and Chow; external only in Bulldog, Newfoundland and Deerhound, but this proves nothing.

† Gruber found a pad (Wulst) in *Sus scrofa* in the external head of *gastrocnemius* but no hemisesamoid, much less an orthosesamoid.

‡ Several knee-joints of sheep on dissection showed no traces of *fabellae* or *cyamella*.

Rangifer tarandus (reindeer, 2 cases), *Tragulus javonicus*[*] (moose deer, 3 cases), *Cervus elaphus* (red deer), *Connochaetis gnu* (white tailed gnu), *Alces machlis* (moose or elk), *Cervus davidianus* (David's deer), *Cervus puda* (Puda deer), *Hyomoschus aquaticus* (African chevrotain), *Cervus capreolus* (roe, 2 cases), *Hydropotes inermis* (Chinese water deer), *Strepsiceros kudu* (koodoo), *Auchenia pacos* (alpaca), *Auchenia vicugna* (vicugna), *Sus scrofa* (Indian wild boar, 3 cases), *Dicotyles labiatus* (white lipped peccary, 2 cases), *Phacochaerus africanus* (Aelian's wart hog), *Hippopotamus amphibius* (2 cases), Baird's tapir, *Equus zebra, Equus asinus, Camelus bactrianus, Camelopardalis giraffa* (Nubian giraffe), *Elephans indicus, Rhinoceros unicornis, Rhinoceros sumatrensis, Bos taurus* and also *Equus caballus,* Orlando (the thoroughbred race-horse) and numerous other ungulates.

In the face of the large number of skeletons of *Cervidae* examined, it seems hard to believe that the external *fabella* has been removed in all these cases, i.e. that it can be, as Meckel asserted, universal in *Cervus*[†].

We have dissected a specimen of a young *Tragulus,* probably from Malasia, but found no *fabellae* nor indeed any sesamoids of the knee-joint. In our opinion an indication of the ancestral history.

Apart from *Cervus, Hyrax* is the only ungulate with sesamoids of the knee-joint. According to Blainville both *fabellae* are present, but Meckel and Brandt credit it only with the external *fabella.* We first examined two skeletons. On one *Hyrax dorsalis,* there was no trace of a *fabella* left, if there ever had been any; on the other *Hyrax capensis,* there was a small external *fabella.* Murie and Mivart in their "Myology of *Hyrax capensis*[‡]" describe *gastrocnemius, plantaris* and *popliteus,* but do not refer to any sesamoids. We were able to examine further one knee-joint of *Hyrax* with certain of the muscular attachments (see Plate XX, Fig. 45). Unfortunately the popliteal tendon had been cut short before it passed over the fibula so it is impossible to say whether a *cyamella* ever existed. The external *fabella* was present, but *gastrocnemius* had shrunk in drying, so that the sesamoid was lifted off the external condyle. There is a slight depressional facet on the articular surface of the internal condyle suggesting the possibility of a mesial *fabella.* There is, however, no doubt about the existence of the external *fabella.* In another mounted specimen of *Procavia,* we have found not only the external *fabella,* but an external anterior *lunula.* These facts provide at least suggestions for the reclassification of the *Hyracoidae.* Apart from the *Cervidae* and *Hyracoidae*—where the presence of the external *fabella* may throw light on their evolutionary history—we are forced to the conclusion that the large (and mixed!) order of the ungulates presents no sesamoids of the heads of *gastrocnemius* or *popliteus.* The absence of the *fabellae* in ungulates has been frequently noticed[§], but so far we believe no stress laid on its evolutionary importance.

[*] We failed to find any sesamoid of the knee-joint on dissecting a young *Tragulus*: see below.

[†] On the fossil *Megaceros hibernicus* (Irish deer) we were unable to find any trace of a *fabella.*

[‡] *Proc. Zool. Society,* 1865, p. 350.

[§] Meckel, Gruber, etc. See also *Journal of Anatomy and Physiology,* Vol. XXXII. p. 750, 1898.

(11) *Pinnipedia.*

No sesamoids of the *gastrocnemius* were found by Gruber* in *Phoca* sp.? He thus confirmed an earlier statement of Meckel† that the *fabellae* were absent in seals. Again reminding the reader of the unreliability of evidence drawn from articulated skeletons, we may note that the following articulated skeletons were examined without finding traces of *fabellae*: *Otaria stelleri* (Steller's sea lion), *Stenorhynchus serridens* (saw-toothed seal), *Cystophora cristata* (bladder-nosed seal), *Otaria falklandina* (Falkland fur seal), *Phoca vitulina* (common seal), *Phoca greenlandica* (the harp seal), *Phoca hispida* (ringed seal), *Balaenoptera rostrata* (lesser fin whale), *Odoboenus rosmarus* (walrus), *Macrorhinus leoninus* (elephant seal), *Otaria jubata* (southern sea lion).

In *Otaria californiana* there is small process or upward growth where articular surface of external condyle meets popliteal area, but it is not sesamoidal in character. We dissected, however, a knee-joint of *Otaria australis* (South American fur seal) and found no such process. There is nothing, therefore, in our observations inconsistent with the view of Meckel that the *Pinnipedia* have no *fabellae.*

(12) *Chiroptera.*

Meckel‡ asserts that the bats have only the external *fabella.* Owen§ says that *Vespertilio murinus*, *Pteropus*, and *Galeopithecus* have both external and internal *fabellae*, while Gruber says that *Galeopithecus* has neither *fabella.* Blainville‖ asserts the existence of a sesamoid in the tendon of *popliteus* in the case of *Vespertilio L.*, i.e., of a *cyamella.* Humphry¶ dealing with the myology of limbs of *Pteropus* and treating of *gastrocnemius* writes: "There is a minute ossicle in the outer head. I cannot find one in the inner head." The not unusual statement is that the sesamoids, the patella and even the semi-lunars are wanting. The above statements suggest that *fabellae* and *cyamella* exist occasionally or in minute forms. Parsons** writing of the *Chiroptera* says no movement except extension and flexion is allowed in fruit bats and there are no traces of the semilunar cartilages; the patella is absent. "In the long-eared bat (*Plecotus*) which will serve as an example of the insectivorous bats the knee-joint does allow a certain amount of rotation and in it semilunar cartilages are found as very delicate rings. This bat resembles the fruit bat, however, in the absence of any trace of a patella."

On the other hand the bat *Cynopterus marginatus* appears in the specimen (R. C. of S. Museum A. 3396) we were able to examine to have an ossified patella, and there might be other ossifications in the knee-joint, but it was not possible to say from this specimen. Gruber†† also found the external *fabella* in *Phyllostoma hastatum*, but failed to find it in *Pteropus* sp.? Besides the above *Cynopterus* we have obtained and examined a considerable number of knee-joints of bats—principally

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* *Loc. cit.* p. 60.

† *Loc. cit.* S. 634.

‡ *Loc. cit.* S. 634.

§ *Anatomy of Vertebrates*, Vol. II. p. 358.

‖ *Ostéographie des Cheiroptères*, Tom. I. Fasc. 5, p. 30, 1840.

¶ *Journal of Anatomy and Physiology*, 1869, p. 313.

** *Ibid.* Vol. XXXIV. p. 310, 1900.

†† *Loc. cit.* p. 55.

Pteropus—having the muscles attached, but we have failed to find any sesamoids. It is probable that a microscopic examination of sections from moist material would lead to more conclusive results, and, perhaps, indicate minute patches of hyaline cartilage hardly appreciable by ordinary dissection. For our present purposes, however, such an investigation would be very unlikely to change the significance which can be drawn from the results for *Chiroptera*. In this order the sesamoids of the knee-joint appear occasionally, as in the higher primates, or in minute forms and are vestiges of a complete system of patella, *fabellae*, and *cyamella*, which belonged to their evolutionary ancestors. Even in this case which is merely vestigial, it is worth while noting the greater importance of the external *fabella*.

(13) *Insectivores.*

With this order we reach vestiges of a more primitive state of affairs in the sesamoids of the knee-joint. The *lunulae* common in the Rodents and carrying us back to reptilean forms are frequently preserved. In the carnivores and the higher primates they occur only as anomalies or have disappeared entirely. According to Blainville[*] *all* insectivores have both *fabellae*. Owen[†] qualified this by saying that *most* insectivores have both. Meckel[‡] had already remarked that the mole has both *fabellae*, but the hedgehog he reported as having only the external *fabella*. Gruber[§] on the contrary found the mole to have an external *fabella* only. He reports that both *fabellae* are wanting in *Erinaceus europaeus* and *E. auritus*, and again in the shrew mouse, both *Sorex vulgaris* and *S. fodius*. He examined three cases of *Myogale moschata*, the Russian desman. In the first case there were no *fabellae*; in the other two cases no internal but external *fabellae*.

> In den Fällen aber mit Vorkommen des Ossiculum externum sass dieses in einem Ausschnitte am Ende des scharfen Angulus externus über dem Condylus externus und daneben in einer kleiner Grube an der hinteren Fläche der Femur[||].

In the case with no *fabellae* there was a "platter Fortsatz" on the same spot. Gruber found this also in *Myogale pyrenaica* where there were no ossicles. We dissected two moles, *Talpa europaeus*, and found the external *fabella* only; thus our specimens agreed with Gruber's and not Meckel's. The hedgehog (*E. europaeus*) examined by us had both *fabellae* and both lateral and mesial anterior *lunulae* (see Plate XXIII, Figs. 56*a* and 56*b*). Thus Gruber's statement is not universal. In a specimen of *Myogale moschata* we found only a large external *fabella* of unusual shape and size, and in *Myogale pyrenaica* no *fabellae*; these two latter in mounted specimens only. In mounted specimens we found only a large external *fabella* in *Talpa europaeus*, *Macrosceledes* (elephant shrew), *Solenodon cubanus* and *Tupaia javanica*. In a specimen of *Tupaia picta* in our laboratory both *fabellae* are present, and both occur in *Tupaia tana*, the Borneo tree shrew. We have also found both *fabellae* in

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[*] *Ostéographie des mammifères*, Tom. I. Fasc. 4, p. 47, Paris, 1841.

[†] *Anatomy of Vertebrates*, Vol. II. p. 393.

[‡] *Loc. cit.* S. 634.

[§] *Loc. cit.* p. 56.

[||] Gruber notices (*loc. cit.* p. 64, that the external *fabella* in *Myogale* is sometimes fused to femur in a special *Fortsätzchen*. This is the only reported case of ankylosis of a sesamoid we have come across, except in the Marsupialia.

Hylomys suillus dorsalis (see Plate XXIV, Figs. 62 *a* and 62 *b*) and *Rhynchocyon cerni* (long-nosed jumping shrew). Two mounted specimens of the golden mole (*Chrysochloris aurea*) provided no signs of *fabellae*. A mounted specimen of *Potamogale* provided an external *fabella*, and a dissection of *P. velox* confirmed this. In *Ericulus setosus* we found no *fabellae*, but the *cyamella* and two anterior *lunulae*, an unusual combination.

Plate XXIV, Fig. 59, provides a drawing of the lateral aspect of the left knee-joint of *Potamogale velox*. There was no sign of ossification in the popliteus tendon and only the external *fabella* was present. Fibula and tibia are fused at their distal ends.

In *Hylomys suillus dorsalis* (Plate XXIV, Figs. 62 *a* and 62 *b*) both *fabellae* are present and fibula and tibia are again distally fused. There was no *cyamella*, and no *lunulae* could be found.

In the mole only the external *fabella* was present and there was no sign of ossification in the popliteal tendon. No *lunulae* could be discovered, but in such small animals absolute certainty could only be reached by cutting a series of sections of the semilunars.

Parsons* in his paper on the limb myology of *Gymnura rafflesii* notes the presence of an orthosesamoid in the external head of *gastrocnemius*; he does not refer to the existence of *lunulae* or *cyamella*. To sum up, the more primitive forms of the *Insectivora* probably possessed both *fabellae*, a *cyamella*, and mesial and lateral anterior *lunulae*. The external *fabella* has been generally preserved, but the complete system as illustrated in the hedgehog shows signs of disappearance by the loss of one or more members as we also find in the higher Primates or Carnivores. It is, however, very far from being vestigial as in the case of the *Chiroptera*.

(14) *Rodents*.

According to Meckel the marmot, the common hamster, the guinea-pig, the agouti, the jerboa (*Mus sagitta*) and the hare have both *fabellae*, but the beaver, the squirrel, the rat, the dormouse and the Cape mouse (*Aorychus capensis*) only the external *fabella*†. Bartolinus‡ had before Meckel referred to the two *fabellae* in the hare and Tyson to those in the guinea-pig. Owen§ found both *fabellae* in the squirrel as well as a *lunula*. He also found both *fabellae* in *Mus rattus*, the water vole (*Arvicola amphibia*), *Hydromys chrysogaster* (golden-bellied rat) and *Hystrix cristata* (common porcupine). Gruber made a fairly long investigation as to the *fabellae* in rodents. He found both *fabellae* in the following: *Myoxus murinus* (the fat dormouse), *Sciurus vulgaris* (common squirrel), external larger; *Pteromys volans* (? American flying squirrel), external larger; *Tamias striatus* (= *Tamias asiaticus* ?); *Spermophilus citillus* (European souslik); *Mus musculus* (common mouse); *Mus rattus* (common rat), external larger; *Hypudaeus* (? *Mus*

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* *Journal of Anatomy and Physiology*, 1898, p. 322.

† *Loc. cit.* S. 604—5.

‡ See Part I of this memoir, p. 15.

§ *Anatomy of Vertebrates*, p. 384.

amphibius, the water vole); *Lemmus obensis* (Siberian, ? Norwegian, lemming), internal somewhat larger! *Fiber zibethicus* (musquash), external large and internal small; *Dipus jaculus* (? *Alactaga jaculus*); *Spalax typhlus* (mole rat); *Lepus timidus*[*] (hare), external in facet on external condyle, internal in groove, but this may happen with external; *Lepus cuniculus* (rabbit), internal small as compared with external; *Cavia* (guinea-pig), external larger; *Dasyprocta aguti*, both as hemi-sesamoids[†] (hyaline cartilages). On the other hand in a *young* specimen of *Castor fiber*, he found neither and this was also the case in *Cercolabes prehensilis* (tree porcupine), although *gastrocnemius* was very fully developed. In *M. glis* Gruber found the external *fabella* only, articulating on condyle. He examined three kinds of *Cricetus* (hamster) and found in one both *fabellae*, in a second the external only, and in a third neither.

We now come to our own investigations. In the authorities cited above we have no records of the presence of the *cyamella* and only the single reference of Owen to the presence of a *lunula* in the squirrel.

A dissection of the common rabbit showed both *fabellae* and the *cyamella* but no *lunula* (see Plate XXIV, Fig. 58). In a mounted skeleton, however, we found both *fabellae*, the *cyamella* and both anterior *lunulae*. A dissection of the common squirrel (two specimens) showed both *fabellae*, the *cyamella* and an anterior mesial *lunula* (see Plate XXIII, Fig. 55 *b*). In a third very young squirrel the lateral *fabella* was found, but no mesial had yet developed (no microscopic examination made); the *lunula* was well developed[‡]. In the African squirrel (*Paraxerus jacksoni*) we found both *fabellae*, the *cyamella* and the anterior mesial *lunula* (see Plate XXIV, Figs. 60 *a* and 60 *b*).

In the domestic mouse both *fabellae* and both anterior *lunulae* but no *cyamella* were found; the smallness, however, of the knee-joint renders (without microscopic examination of sections) the discovery of the sesamoids rather precarious.

In the musk rat (*Fiber zibethicus*) we found both *fabellae*, two anterior *lunulae*, of which the mesial is under the ridge of the patellar depression, and one posterior lateral *lunula*. There was no trace of a *cyamella*, and it is possible that it does not exist in the musk rat or is replaced by this posterior *lunula* (see Plate XXIV, Figs. 61 *a* and 61 *b*).

Turning to mounted specimens we found both *fabellae* in the following: *Trichys guentherai* (Gunther's porcupine), *Lagostomus trichodactylus* (Viscacha[§]) in two specimens, *Thrynomys swindernianus* (cave rat), *Mus fuscipes* (brown-footed rat), *Mesembriomys hirsutus* (Gould's jerboa rat), *Microtus amphibius* (water vole), *Alactaga decumana* (Kirchig jerboa), *Alactaga acontium* (Siberian jerboa), *Spermophilus guttatus* (a souslik), *Sciuropterus volucella* (North American flying squirrel), *Dasyprocta aguti* (golden agouti)*, *Cavia porcellus* (guinea-pig), *Myopotamus coypus* (coypu), in a second specimen only the external *fabella* was preserved, *Anomalurus fraseri*, in this case the *cyamella* had been preserved.

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[*] Mivart and Murie, *Proc. Zool. Society*, 1866, p. 413, state that the hare differs from the guinea-pig by having neither *fabella* (!).

[†] We have found orthosesamoids in our specimen.

[‡] We also found only the lateral *fabella* in a mounted specimen of the common squirrel, but this is hardly evidence even of the occasional absence of the mesial. Cf. Meckel's statement p. 53.

[§] There is a double-sized lateral and a smaller mesial *fabella*.

In a skeleton of *Dolichotis patachonica* (Patagonian cavy) no *fabellae* remained, but there were exceedingly well-marked depressions for the *fabellae* on the condyles†, and in another skeleton of *Dasyprocta aguti* where the two *fabellae* had disappeared their positions were well marked by depressions on the condyles. There were well developed pits also on the condyles, almost certainly for *fabellae*, in *Hystrix leucura*. Occasionally when the *fabellae* were not traceable, *lunulae* had been preserved; thus in *Hydromys chrysogaster* (golden-bellied rat) we found both anterior *lunulae*. In another specimen, however, we found both *fabellae* and the anterior *lunulae in situ*. These are reproduced in Plate XXIII, Fig. 57 *a*. The *lunulae* of the anterior border of the semilunar cartilages existed in another skeleton of *Dolichotis patachonica*†. In a mounted specimen of *Hystrix cristata* (crested porcupine) the *fabellae* and *cyamella* failed but there appeared to be an external anterior *lunula*, while in *Synetheres insidiosus* (a South American porcupine) there were, if there ever had been any, no remaining sesamoids, not even the *lunulae*.

Parsons, who has dealt at length with the myology of the rodents, wrote as follows in 1894‡ of the *Hystriomorphinae*:

> The presence or absence of the *fabellae* does not seem to depend on the affinities of the animal, as they are large in *Aulacodus* on both sides, while in *Myopotamus*, only the outer one is present. In *Dasyprocta* they are both present, in *Calogenys* both absent.

We have found in a specimen of *Myopotamus* both *fabellae* present.

Again:

> In the *Sciuromorphinae*, however, they were found in every case except that of *Castor canadiensis* (*Sciurus*, *Pteromys*, *Xerus*, *Spermophilus*, *Arctomys*, *Castor*).

In a paper of 1896§ on the "Myology of the Rodents," Parsons writes that all except fam. *Spalacidae* (*Rhizomys*, *Georychus*, *Bathyergus*) have two *fabellae*.

It will be seen that a good deal of work remains to be done on the rodents. It is not easy to obtain adequate material to determine an isolated problem of the knee-joint like the present. It is to be hoped that myologists in the future may pay attention to the existence of *cyamella* and *lunulae* as well as of the *fabellae*. But our experience shows us that without a most careful examination, which in many cases ought to be microscopic, it is by no means easy to ascertain the presence or absence of these sesamoids even in most specimens of the smaller rodents. Further, it is quite clear from the material we have gathered together that persistent presence or absence in the same species cannot be asserted from the examination of isolated specimens.

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* Windle found both *fabellae* in *Dasyprocta isthmica*, *Journal of Anatomy and Physiology*, 1896—97, p. 352, and Mivart and Murie, *Proc. Zool. Society*, 1866, found both in *Dasyprocta cristata*.

† Windle, *Journal of Anatomy and Physiology*, 1896—1897, p. 352, says he found only the lateral *fabella*.

‡ "Myology of the *Sciuromorphinae* and *Hystriomorphinae*," *Proc. Zool. Society*, 1894, p. 291.

§ *Proc. Zool. Society*, 1896, p. 181.

The *Rodentia* undoubtedly show, however, a greater persistency of the *fabellae* than the *Insectivora*, and what is more a greater prevalence of *cyamella* and anterior *lunulae*. Had these been directly searched for by others as well as ourselves, we believe their prevalence would have been much more emphasised in the reader's mind. The appearance in a few cases of the external posterior *lunula* is also of much suggestiveness. We have not, however, yet come across a case of this *lunula* co-existing with the *cyamella*[*]. In the rodents we have further evidence of the difference in origin of the two *fabellae*, partly in the fact that when both are present the lateral is larger and more important than the mesial, it being as in man an attachment of more than one muscle, and partly in the second fact that, in those species which have a single *fabella* only, it is invariably the mesial which fails.

Before we pass to the *Edentates* as linking up the groups we have already discussed we must consider the Primates themselves and ascertain whether they obey the same general law, namely that the lower and more primitive forms are multi-sesamoidal with regard to their knee-joints, while the higher types have retained fewer, or if they exhibit any at all it is only as anomalies.

(15) *Primates.*

We have already discussed Man. The lateral *fabella* occurs as an anomaly and may be either a hemisesamoid or an orthosesamoid. The mesial *fabella* as an orthosesamoid has not yet been satisfactorily demonstrated[†]. It is clearly far rarer than the lateral *fabella*. There is evidence for the *cyamella* as a very rare anomaly and possibly still more rarely of *lunulae*. The comparative frequency of these anomalous sesamoids of the knee-joint in men of different races would be a study of considerable interest and might give valuable hints. It should not be hard by means of skiagrams to obtain something like comparative figures for, say, Japanese, Negroes[‡], Australians and American Indians which might be set against our English work.

Turning to the *Anthropoidea* we meet the difficulty so often referred to, namely, that the larger skeletons are apt to be too much cleaned for present purposes.

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[*] The reader will have noted that we have dropped the adjective "lateral" in this latter portion of our work. So far we have no evidence beyond Pfitzner's for cats and our own still more doubtful for man of the existence of the mesial *cyamella* even as an anomaly.

[†] In 1909 Lunghetti asserted that he had found the mesial *fabella* in two cases, but he does not give evidence that they were orthosesamoidal, *Internationale Monatschrift für Anatomie und Physiologie*, Bd. XXVI. S. 71. L. Stieda in 1902 found and exhibited to the German Anatomical Society (*Anatomischer Anzeiger. Verhandlungen der Anatomischen Gesellschaft. Ergänzungsheft zum Bd.* XXI. 1902, S. 127) a mesial *fabella* from a human cadaver. It articulated with the mesial condyle, and was enclosed in the knee capsule. It could be clearly seen and felt. Stieda says it was 1 cm. about in diameter, and therefore a very large size for even a lateral *fabella*. He did not apparently extract the *fabella* and so make himself absolutely certain that it was ossified. He had possibly not fully studied the difficulties of the subject for he describes (S. 128) Heister's figure as "eine sehr gute und lehrreiche Abbildung"! See our p. 18 and Plate II.

[‡] Chudzinski according to Poirier holds that the sesamoid bone of the *inner* head of *gastrocnemius* is invariable in the Negro! We have been unable to verify the reference and very strongly doubt the truth of the assertion. Dr E. C. Derry kindly examined for us two negro cadavers in his dissecting room and found in both cases neither mesial nor lateral *fabellae*.

Meckel does not seem to have examined the *Anthropoidea* although he deals fairly fully with the lesser apes. Gruber has also no data. Owen's paper of 1866 contains no reference as to the sesamoids of the knee-joint*. Macalister in his paper on "The Muscular Anatomy of the Gorilla"† writes that

> The popliteal muscle had a sesamoid bone or cartilage; it [the muscle?] was about as large proportionately as in man.

Thus Macalister seems the first to have noted the *cyamella* in the gorilla. We have already drawn attention to the fact that Camper had found it in the orang in 1791. Macalister in a further paper‡ dealing with the chimpanzee, remarks:

> The popliteus was small and had no sesamoid nodule in its tendon thereby agreeing with Wilder's and differing from Vrolik's specimen. Trail did not find it [? *popliteus*] present.

Wilder in his paper on "The Comparative Myology of the Chimpanzee"§ states, when dealing with *popliteus*, that he "could not find the cartilaginous nodule in the external lateral ligament where the muscle arises." It is not clear that this really does refer to the *cyamella*. Wilder continues: "Trail and Tyson could not find the muscle, but it was present in Vrolik's chimpanzee and in the gorillas of Wyman and Duvernoy" (*l.c.* p. 375). The "it" of Macalister's sentence just cited should refer to *popliteus*, otherwise Macalister has misread Wilder, who is referring to the muscle and not to the sesamoid‖.

It would seem then that of the anthropoids the gorilla, chimpanzee and orang have no *fabellae* and that gorilla and orang have the *cyamella*. The chimpanzee on the weight of the evidence published above does not seem to have the *cyamella*. Reports that the chimpanzee has it arise from a not unnatural reading of Macalister's loose wording, at most it can only be as an anomaly. Thus even in this respect man approaches more closely to the chimpanzee than to the gorilla or orang.

By the courtesy of Sir Arthur Keith we were able to dissect the knee-joint of a chimpanzee. We found no *fabellae*, and not a *cyamella*, but a scarcely perceptible thickening of the popliteal tendon¶. We procured and dissected the knee-joints of two orangs. In neither case was either *fabella* present but in both cases there was a large *cyamella*: see Plate XXVI, Figs. 68 and 69. Sir Arthur Keith kindly allowed one of us to examine his manuscript thesis of 1894 entitled: "The Myology of the Catarrhini. A Study in Evolution." It is a most valuable work of 600 pages presented to the Library of the Royal College of Surgeons in 1919. In this work he notes that he has not found the *fabellae* in gorilla or orang, but he found the *cyamella* (described as sesamoid in the tendon of *popliteus* above external tibial tuberosity) in both, but not in the chimpanzee (p. 307). On the other hand he states that he did find in a chimpanzee (p. 297) a mesial *fabella*—i.e. the inner tendon of head of *gastrocnemius* contained a sesamoid. This result is of considerable importance. The consensus of opinion is against the occurrence of any *fabellae* in the chimpanzee but the occasional anomalous appearance of a *fabella*, especially a mesial hemisesamoid, would be exactly what we might anticipate with the close relationship that exists between man and the chimpanzee.

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* "Osteological Contributions to the Natural History of the Anthropoidal Apes, No. VII." *Trans. Zool. Soc. London*, Vol. V. The femora of gorilla, chimpanzee and the orang are discussed on p. 14, *et seq.*

† *Proc. Royal Irish Acad.*, Vol. I. 2nd series, p. 505. Dublin, 1870, p. 74.

‡ "Myology of the Chimpanzee and other Primates," *Annals of Natural History*, 1871, p. 9.

§ *Boston Journal of Natural History*, Vol. VII. p. 375, 1861.

‖ Gruber says Vrolik did *not* find the sesamoid; and we think Gruber naturally read Macalister's sentence to indicate that Vrolik had found the sesamoid and he wished to contradict Macalister.

¶ Our chimpanzee was like those of Wilder, Macalister and Vrolik in the fact that *popliteus* was present.

Hylobatinae. Hepburn in his memoir on "The Muscles and Nerves of the Anthropoid Apes" (*Journal of Anatomy and Physiology*, 1892, p. 337), found a sesamoid bone developed in each tendon of origin; in dealing with *popliteus* he makes no mention of the existence of a sesamoid, which he would have been pretty certain to have done had it existed. We dissected the knee-joint of a gibbon (*Hylobates muelleri*) and found the mesial *fabella* only, no *cyamella** and no *lunulae*: see Plate XXVII, Fig. 72. This result is in full accord with Sir Arthur Keith's expressed in his thesis: "Gibbon: sesamoids extremely variable even in adult animals. There may be one in each head or both may be absent or either may be absent" (p. 297). In Diagram 75 of Sir Arthur Keith's thesis figures the knee-joint of a gibbon, the internal head of *gastrocnemius* with large, the external head with minute sesamoid. He has never observed the *cyamella* in the gibbon. The existence of individual gibbons in which the mesial *fabella* only appears, while it may seem like the exception which proves the rule, is not so really, for the rule is that no species occurs in which the mesial *fabella* is invariably present and the lateral *fabella* invariably absent. The invariable presence of the lateral and invariable absence of the mesial *fabella* is as we have seen characteristic of certain species†.

The mounted skeletons of *Anthropoidea*, e.g. those at the British Museum (Natural History) and at the Royal College of Surgeons, are all "too clean" to show the sesamoids of the knee-joint. It may be hoped that in future the *cyamella*, where it occurs, will be preserved and mounted as well as the *fabellae*, both in these cases and those of the Old and New World Monkeys, although very often the *fabellae* are preserved in the latter.

Simiadae (Old World Monkeys). We have already seen that the existence of both *fabellae* in the Old World Apes was known to Sylvius and Riolanus (see our pp. 12—13). Meckel gives a fairly extensive list of lemuroids, New World and Old World Monkeys in which he had observed both *fabellae*‡. Gruber notes that he had found both in the genera *Cercopithecus*, *Inuus*, *Cynocephalus*§, and *Cebus*

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* The tendon of *popliteus* was "horny," but there was no sesamoid.

† It is worth noting that even in the gibbon Keith (*Thesis*, p. 298) found the lateral *fabella* more frequently present than the mesial.

‡ *Loc. cit.* S. 634—635.

§ We have found both *fabellae* in *Macacus leoninus*, *M. pileatus*, *M. rhesus* (several specimens), *M. inuus* (Barbary ape), *M. cynomolgus* (several specimens), *Cynocephalus anubis*, *M. nemestrinus* (two specimens), *M. speciosus* (Japanese ape), *Cercopithecus lalandii* (two specimens), *Colobus ursinus*, *C. vellerosus*, *Nasalis larvatus* (two specimens), *Semnopithecus orientalis*, *S. entellus*, *Papio hamadryas*, etc. etc. Burdach, Olg and others have noticed other cases from 1838 onwards.

(New World Monkey). In *Cynocephalus* he found sometimes the mesial sometimes the lateral the larger. In the remainder the lateral was invariably the larger. Neither Meckel nor Gruber* refers to the *cyamella* as existing in either *Simiadae* or *Cebidae.*

Keith in the above-mentioned thesis takes *Semnopithecus* as his type. He thus describes the relation of the muscles in his type to the sesamoids:

Gastrocnemius. Origin. *External head*; arises by musculo-tendinous fibres from a sesamoid embedded in the general capsule of the knee-joint and plying over the upper convexity of the external femoral condyle, and from the shaft of the femur immediately above and external to the femoral condyle (p. 296).

Internal Head: from a sesamoid situated similarly to that of the external head and from the shaft of the femur immediately above the internal condyle.

Plantaris. Origin; from the sesamoid in the external head of *gastrocnemius* (p. 304).

Popliteus. Origin. By a rounded tendon from the lateral aspect of the external femoral condyle beneath the external lateral ligament and within the capsule of the knee-joint....There is a sesamoid in the tendon over the external tibial tuberosity (p. 307).

The arrangement of the muscles relative to the sesamoids in *Semnopithecus* as given by Keith is curiously like what we have learnt of the relation of the muscles to the *fabellae* and *cyamella* when they occur in man. This is peculiarly true of *plantaris*, and is evidence, similar to that provided in the memoir on the Femur by Pearson and Bell, that in a number of respects man is closer to the *Simiadae* than to the *Anthropoidea* whether by retaining more primitive characters, or by reverting to earlier types as better suiting his differentiated development.

The *cyamella* as well as both *fabellae* are present not only in *Semnopithecidae*, but in macaques, *Cynocephali* and practically all the *Simiadae*, we have been able to investigate†. Our drawing (Plate XXVII, Figs. 71 *a* and 71 *b*) shows the two *fabellae* and the *cyamella* in *Mycetis palliatus*, both in position and after extraction.

Lastly we note that we have not been able to find *lunulae* in any knee-joint we have examined of the *Simiadae*. Should they occur, we believe their appearance is very rare.

Cebidae (New World Monkeys). Here the problem is somewhat easier than in the *Simiadae.* The bulk of the species being smaller in size our purchased specimens were less "clean," i.e. the muscular attachments remained. We were thus better able to give positive evidence as to the non-existence of *lunulae.*

(i) We found both *fabellae* in *Hapale aurita* (white-eared marmoset), *Midas oedipus*, *M. midas*, *M. ursulus* (two specimens), *M. auritus* (golden marmoset),

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* It is the more noteworthy in Gruber's case for he does refer to a large *cyamella* in *Stenops tardigradus.*

† We have noted *cyamella* in *Nasalis larvatus*, in *Macacus* (the Bonnet monkey), *M. inuus*, etc. and believe that it is general in the *Simiadae*, although usually cleaned off in mounted specimens.

Hapale jacchus (common marmoset), *Jacchus auritus,* and two other specimens (sp. ?) of *Jacchus, Cebus capuchinus* (two specimens), *Cebus* (sp. ?) (two specimens), *Lagothrix humboldtii* (two specimens), *Pithecia satanas* (Black Sahi), *Pithecia.* (sp. ?), *Nyctipithecus, Chrysothrix sciurea* (three specimens).

(ii) In none of these were any *lunulae* to be found.

(iii) We found the *cyamella* definitely in *Hapale jacchus, Jacchus auritus,* in two other specimens of *Jacchus* (sp. ?), in *Midas ursulus* (two specimens), *M. midas, M. auritus.*

We could not definitely assert its absence in *Cebus* or *Pithecia,* or the squirrel monkeys, as the material was less complete.

The case of *Ateles* is also doubtful; two specimens were examined, in neither was a *cyamella* found; one possessed no *fabellae* and the other only an internal one. This may be due to rough usage, or it might emphasise the correspondence with the gibbons which Pearson and Bell noticed in considering the femur of *Ateles.*

While we should have anticipated finding *lunulae* in the more primitive types of *Cebidae,* we have not done so, and conclude that the *lunulae* were lost to the Primates except as occasional anomalies before the separation of *Simiadae* and *Cebidae.* The chief difference between the apes of the New and Old Worlds is that the *Cebidae* (except in the possible case of *Ateles*) have never progressed to the stage of the *Hylobatinae* with loss of *cyamella* and to the stage of the *Anthropoidea* with loss of *fabellae* as well.

Lemuroidea. We naturally turn with much interest to the prosimian group; for the sesamoids of the knee-joint in their case ought to link up with those of the Rodents and Insectivores and the test of this will clearly be the occasional or persistent occurrence of *lunulae* in one or more species.

Here again the expense of procuring moist material, especially when it is to be investigated only for a single point in as wide a range of species as possible, has much handicapped our work*.

We turn first to the lemurs proper and notice the following remarkable results†: Both *fabellae,* the *cyamella* and the lateral anterior *lunula* were found in *Lemur varia, L. catta, L. melanocephalus, L. coronatus, L. macaco leucomystax*‡. There is no doubt therefore that the *Prosimia* add the lateral anterior *lunula* to the *fabellae* and *cyamella* of the *Simiadae.* See Plate XXVII, Figs. 70 and 73.

Turning to *Galago* we have found: *Galago alleni,* both *fabellae,* the external very large, the *cyamella* and the lateral anterior *lunula. G. crassicaudata* exhibited also the two *fabellae**, *cyamella* and lateral anterior *lunula*. Another *Galago* (sp. ?) gave the same result, while a series of mounted specimens provided sometimes (as oversights of the articulator!) the *fabellae*, or the *cyamella* and once a *lunula*.

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* The aid given by the Government Grant Committee to the Study of Pearson and Bell on the femur, for the purchase of primate material, has of course aided us.

† Meckel notes merely the existence of both *fabellae* in *L. mongoz,* and *L. albifrons.* Gruber states that *Stenops tardigradus* lacks both *fabellae* but has a large articulating sesamoid in the tendon of *M. popliteus.*

‡ Femora without the semilunars of *L. rubiventer, L. niger,* and *L. macao varius* showed both *fabellae* and in the first case the *cyamella* also remained.

In *Lemur macao niger*, both *fabellae*, the *cyamella* and apparently *both* anterior *lunulae* were present. *Nycticebus javanicus* had also *fabellae*, *cyamella* and lateral anterior *lunula*; a mounted specimen of *Nycticebus tardigradus* retained only the *cyamella*†. Going further we find *Loris gracilis* with *fabellae*, *cyamella* and lateral anterior *lunula*, apparently but difficult to decide definitely without a section there was also a lateral posterior *lunula*; a mounted specimen showed more definitely two *lunulae*.

Perodicticus potto gave us *fabellae*, *cyamella* and lateral anterior *lunula*, and the *cyamella* was confirmed in a mounted specimen of the Calabar potto.

We now reach cases in which we can be more or less definite as to absence of *lunulae* because the semilunars were preserved.

Chiromys (Aye-Aye) dissected gave both *fabellae* and *cyamella*, there were no *lunulae*: see Plate XXVIII, Fig. 74 *a*. A second specimen in the Biometric Laboratory was investigated with precisely the same result no *lunulae*. Mounted specimens show the *fabellae* as a rule; in one we found the *cyamella* preserved. The existence of the *cyamella* in the Aye-Aye was, we believe, first noted by Owen. He makes the important point that "there is a sesamoid in the external lateral ligament of the knee-joint at its insertion into the head of the fibula." (See our Plate XXVIII, Fig. 74 *b*.) He also refers to the *fabellae* in the Aye-Aye. ("On the Aye-Aye." *Trans. Zool. Soc. London*, Vol. v. p. 53, 1866.)

In *Avahi laniger* and *Hapalemur griseus* we found both *fabellae*, definitely no *lunulae*, the *cyamella* failed but might possibly have been removed. A mounted specimen of *Avahi laniger* as well as one of *Propithecus diadema* showed only the *fabellae*. In a mounted specimen of *Lepidolemur microdon* we found only *cyamella* and external *fabella*.

Chirogaleus and *Indris brevicaudata* gave only the *fabellae* and *cyamella*.

Lastly *Tarsius spectrum* has both *fabellae* and the *cyamella*. Curiously enough as in *Galago crassicaudata* the mesial *fabella* may be larger than the lateral, although we have seen specimens mounted having solely the lateral *fabella*. We can only say we have not yet found *lunulae* in *Tarsius*. This is not very strong evidence against their existence, because the semilunars are so small that without fresh moist material carefully sectioned and microscopically examined it would be difficult to give a strong negative. When we resume our results for the *Lemuroidea* we see their great importance. The non-appearance of the *lunulae* in the marmosets is more or less accounted for, because in the lower stage of the lemuroids while they are found, they are not universal; the *lunulae* have already begun to disappear, although the type lemuroid may be said to be that which has both *fabellae*, the *cyamella* and the lateral anterior *lunula*. A further point which will develop its interest as we proceed is that noted by Owen in the Aye-Aye, namely the situation of the *cyamella*. We reproduce, Plate XXVIII, Fig. 74 *b*, Owen's drawing. The reader will note how in a marvellous manner the *cyamella* and the lateral *fabella* are being brought into close association. The bearing of this on the origin of both of them will be seen in the sequel. The *cyamella* articulates with the head of the fibula and the possibility of the lateral *fabella* articulating with the *cyamella* is seen to exist*. Fig. 74 *a* shows our actual dissection; the head of the *fibula h* is in contact with the *cyamella f*. The two branches of *gastrocnemius a* and *b* have been deflected to show the *fabellae c* and *d*, as dark patches; the positions in which they rest on the condyles are also indicated.

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* Mesial larger than lateral.

† Mivart and Murie (*Proc. Zool. Soc. London*, 1865, p. 129) in their "Anatomy of *Nycticebus tardigradus*" note of *M. popliteus* that it is inserted by a very strong tendon containing a large sesamoid bone...into the depression outside the lateral condyle. They do not mention when discussing *M. gastrocnemius* the existence of sesamoids therein.

Plate XXVIII, Fig. 77 gives the dissection of the knee-joint of *Indris brevicaudata* and shows the *fabellae* and *cyamella* in position.

Plate XXVII, Figs. 70 *a* and 70 *b* show in *Lemur varia* the type knee-joint of the lemurs. *a* is the external, *b* the internal *fabella*, *c* the *cyamella* on the head of the fibula and *d* is the lateral anterior *lunula*. Figs. 75 and 73 show with the same notation the same four sesamoids in *L. catta* and *L. melanocephalus*.

Plate XXVIII, Fig. 76 gives the lateral aspect of the dried knee-joint of *Perodicticus potto*. In this case no *fabellae* were present, having most probably been knocked off. The *cyamella* (*cy.*) is seen resting on the head of the fibula, the popliteal tendon sends a branch down to the head of the fibula. On the posterior and upper face the *cyamella* is concave, and this hollow seems designed for the *fabella* to rest in. The anterior external *lunula* is in its usual position, i.e. in the semi-lunar cartilage just in front of the popliteal tendon.

The main point of interest in the lemuroids is undoubtedly the link that the *lunula* presents with the Rodents and Insectivores. But the close relationship which the forms and positions of *cyamella* and lateral *fabella* in the lemuroids bear to a continuous articulating system connecting the head of the fibula with the lateral condyle of the femur is full of suggestiveness. This relationship of lateral *fabella* and *cyamella* explains we think to some extent Gruber's confusion of the two when as in man only one occurs and then as an anomaly.

(16) *Edentates.*

Before we discuss the very peculiar sesamoidal knee-joint characters of this order it seems desirable to be clear on a point which is rather obscure in some of the earlier writers, who are liable to confuse the *cyamella* with the lateral *fabella*.

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* It is worth while comparing the drawing of the cat's knee-joint on our p. 48 with Owen's of the Aye-Aye's knee-joint. The manner in which with flexed limb the lateral *fabella* and *cyamella* come in contact will be obvious.

The following rules appear to us to hold for the somewhat heterogeneous material classed as *Edentata*.

(i) *Lunulae* may occur.

(ii) There are no cases at all of the mesial *fabella* (with or without the lateral *fabella*) occurring*.

(iii) When the *cyamella* occurs it is very extensive and when it occurs there is no lateral *fabella*.

(iv) Conversely when the lateral *fabella* occurs there is no *cyamella*.

(v) There are cases in which no sesamoids whatever of the knee-joint have been found.

We have accordingly reached a stage in which the mesial *fabella* has not been evolved, for it does not seem to exist in any earlier types. Further we have reached a stage where a non-sesamoidal type of *Monodelphia*—a type afterwards so widely developed in the *Ungulata*—is seen alongside a sesamoidal type afterwards so widely developed in *Rodentia, Insectivora, Primata* and *Carnivora*. It would seem as if the *Edentata* as modern representatives of these primitive *Monodelphia* must be from the knee-joint sesamoidal standpoint most suggestive from their very heterogeneity. Meckel speaks of the external *fabella* only as existing in the Edentates, and cites as examples the Anteater and Sloth (Aï). He does, however, say that this external *fabella* "indessen mehr dem Kneekehlmuskel gehört†." He also found this sesamoid very large in the Edentates, much larger than in other animals, a remark we can fully confirm.

Gruber‡ found in *Bradypus tridactylus* (the three-toed sloth) and in *Dasypus sexcinctus* (six-banded armadillo) no sesamoids in the heads of *gastrocnemius* or in the tendon of *popliteus*, but in *Myrmecophaga* there was in the tendon of *popliteus* a sesamoid articulating with the *capitulum fibulae*.

Gruber's result for *Bradypus* is somewhat surprising, for while there are no *fabellae* there exists, as Blainville first noted, a great *cyamella*; there is in addition a *lunula*. The point is well put by Mackintosh in his paper "On the Myology of the Genus *Bradypus*"§ that while there are no *fabellae* in *gastrocnemius*: "There is a large wedge-shaped *fabella* [i.e. *cyamella*] in the origin of this muscle [i.e. *popliteus*], the tibial surface of which is the larger and articulates both with the femur and the tibia."

We are, we think, reaching a stage of evolution in which lateral *fabella* and *cyamella* have coalesced and form a single large sesamoid. This large sesamoid may articulate with both femur and tibia as in *Bradypus*, or form a link between the femur and the *capitulum fibulae* as in the Anteater‖. Gruber, who never clearly distinguished between lateral *fabella* and *cyamella*, remarks* that in animals in which the *ossiculum* in *gastrocnemius externus* articulates on the head of the fibula, *popliteus* springs from the knee-capsule and from the *capitulum fibulae* not from the femur itself. We have indeed lost the distinction between the two sesamoids although we shall sometimes continue to speak of the *cyamella* as the single large sesamoid of the Edentates, because it is peculiarly associated with the *popliteus*†. The transition stage of the lemuroids in which *fabella* and *cyamella* were coming into close contact now provides much suggestiveness, which will be again emphasised when we come to the Marsupials.

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* Compare what is stated later as to *Orycteropus*, p. 65.

† *Loc. cit.* p. 635.

‡ *Loc. cit.* p. 62.

§ *Proc. R. Irish Acad.* Vol. I. *Science*, 2nd Series, p. 528.

‖ This alternative, tibio-femoral or fibulo-femoral, link of the compound sesamoid might conceivably have bearing on the appearance of *fabellae* in *both* heads of *gastrocnemius*.

In Plate XXIII, Fig. 55 *a* the reader will find a photograph of *Tamandua tetradactyla*‡ with the *cyamella* attached to the popliteal tendon originating in the popliteal groove on the lateral face of the external condyle. It will be easy to see how a not too careful articulator can mount this sesamoid on the surface of the external condyle. The *cyamella* itself articulates on the lateral side with external articular surface of the tibial head. This head projects over and downwards on the head of the fibula, which does not articulate with the femur. The large *cyamella* bears some trace of being a possible compound, i.e. *cyamella* and *fabella*. We have found this *cyamella*—without *fabella*—in:

Bradypus tridactylus (two mounted specimens), *Bradypus arctopithecius*, *Choloepus hoffmanni*, *Choloepus didactylus* (two specimens where the *cyamella* appears to be almost in the position of an anterior *lunula*), *Myrmecophaga tamandua*, *Manis dalmanni* and *Manis javanica*.

There is, we think, no doubt that in *Manis* we are dealing with a *cyamella* and not a lateral *fabella*. Owen, however, speaks of this sesamoid in *Manis* as an external *fabella* (*loc. cit.* p. 409). Windle and Parsons in their paper "Myology of the Edentates"§ remark under *gastrocnemius*: "It is interesting to notice that all observers have recorded the absence of *fabellae* except in the *Orycteropidae*" (p. 1004). This statement seems to overlook Owen and Gruber's statements as to *Manis*, and Macalister's with regard to *Tamandua* and *Myrmecophaga didactyla*.

In his paper‖ on the "Myology of *Bradypus tridactylus*" Macalister writes of the heads of *gastrocnemius*, and says that there are no sesamoids in the origins of the muscle as there are in *Tamandua* and *Myrmecophaga didactyla*. He then continues that Meckel refers to the Aï as possessing one of these in its origin and in the *Megatherium* one of these appears to have existed for the outer head of the *gastrocnemius*. Later referring to *popliteus* Macalister states correctly that the sesamoid, a large one, of *Bradypus* lies in its tendon*, and then says that *popliteus* contains no sesamoid in *Tamandua*, *Orycteropus* and *Dasypus*. We feel sure he is wrong in the first case, the sesamoid of *Tamandua* is a *cyamella*. He is right about *Dasypus*. Owing to the kindness of Sir Arthur Keith it was possible for us to dissect a knee-joint of *Dasypus sexcinctus*; no *fabellae* were found, and only a cartilagenous thickening of the popliteal tendon, which it was not even possible to consider as a hemisesamoid†. There is no doubt, we think also, that the sesamoid in the fossil *Megatherium cuvieri* in the museum of the Royal College of Surgeons is a *cyamella* not a *fabella*. This fossil possesses also a very fine lateral anterior *lunula*: see Plate XXV, Fig. 66. Owen makes no reference to it, and we have not found any mention of it elsewhere. This sesamoid like the *cyamella* rests on the fibular articulating surface, but we consider that it would have been in the anterior border of the lateral semilunar. The so-called "fabella" is a parafibular sesamoid, it does not lie in the popliteal sulcus, but the tendon of popliteus would pass directly to it; it is not on the posterior surface but the lateral surface of the external condyle. It represents really something anterior to the differentiation of parafibula into *cyamella* and *fabella lateralis*.

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* *Loc. cit.* p. 65, (15).

† It would be better to speak of it as the parafibula, except that in certain cases it has changed its position so as to articulate with the tibia.

‡ Macalister in his "Myology of *Bradypus tridactylus*" (*Annals of Natural History*, 1869, p. 15) speaks of the large sesamoid in the tendon of *popliteus* and states that it does not seem to occur in *Tamandua* (!).

§ *Proc. Zool. Soc. London*, 1899, p. 990.

‖ *Annals of Natural History*, 1869, p. 15.

Windle and Parsons' statements as to the sesamoids of the Edentates, namely that the

(*a*) *Bradypodidae* have no *fabellae* but a *cyamella* (p. 1010),
(*b*) *Myrmecophagidae* have no *fabellae* but a *cyamella* (p. 1011),
(*c*) *Manidae* have no *fabellae* but a *cyamella* (p. 1013),
(*d*) *Dasypodidae* have neither *fabellae* nor *cyamella* (p. 1012),

seem to us to represent the facts.

With regard to the *Orycteropidae* there appears to be some diversity of opinion. Humphry in his paper on the "Myology of *Orycteropus capensis*‡ (Aard Vark)" states that the three heads of *gastrocnemius* arise from the outer and inner condyles of the femur and from the head of the *fibula*, [? *soleus*], and that the two former have both sesamoids, i.e. *fabellae*. Galton in his "Myology of *Orycteropus capensis*"§ mentions only a sesamoid in the outer head of *gastrocnemius*, and cites Owen (*Anatomy of Vertebrates*, Vol. II. p. 409). He speaks of this *fabella* as "behind the outer condyle of the femur," and seems to think it corresponds exactly to what Meckel observed in *Choloepus didactylus* "though not mentioned by him in connection with this [*gastrocnemius*] or any other muscle." This is overlooking what Meckel himself wrote about the closer association of the sesamoid with the *popliteus* (see our p. 63)‖. And if *Orycteropus* really resembled *Choloepus*, then it would be a

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* The drawing of the skeleton of *Bradypus tridactylus* in Parker and Haswell's *Text-book of Zoology*, p. 529, shows the *cyamella* and the *lunula*.

† In one mounted specimen of *Dasypus sexcinctus* facets on the condyles were observed which some might interpret as vestiges of *fabellae*.

‡ *Journal of Anatomy and Physiology*, Vol. II. p. 313.

§ *Trans. Linnean Soc.* Vol. XXVI. p. 594.

‖ Mackintosh ("Muscular Anatomy of *Choloepus didactylus*," *Proc. Royal Irish Academy*, Vol. II. 1875—77, p. 75) states definitely that *popliteus* has a large *fabella* [i.e. *cyamella*] in the tendon of origin.

cyamella and not a *fabella* with which we are concerned*. The maximum confusion seems to be introduced by Macalister's paper of 1875 †. Writing of *popliteus* in *Chlamydophorus* he says: "I found no sesamoid bone in its tendon, as it lies under the external lateral ligament, nor does Hyrtl mention the existence of one. In the three-toed Sloth there is a large sesamoid bone. It is similar in *Choloepus*. There is no sesamoid bone in the *Orycteropus*, but there is in *Cyclothurus* and *Rholidotus*. There does not appear to be one in *Myrmecophaga* or in *Tamandua*" (p. 266). The latter statement is incorrect. The statements as to *Bradypus* and *Choloepus* are correct, but Macalister adds *Chlamydophorus* to *Orycteropus* as without *cyamella*.

Turning to *gastrocnemius*‡ he says that *Chlamydophorus*§ has the usual two heads neither of which possesses a sesamoid. There are no sesamoids in *Bradypus*, but Meckel found one in his specimen [we have already seen that Meckel found a popliteal not a *gastrocnemic* sesamoid]. No sesamoids exist in *Choloepus didactylus*. In *Orycteropus* there is a sesamoid bone in the outer head. [Humphry says he found a sesamoid in *both* heads!] A similar one exists in *Cyclothurus* and *Tamandua*. [This last statement is incorrect with regard to *Tamandua*, it may be correct but we have found only the *cyamella* in three limbs of *Cyclothurus*. If it were correct *Cyclothurus* would be the one Edentate that has both *cyamella* and lateral *fabella*.] As *Chlamydophorus* has neither *fabellae* nor *cyamella*, it must be classed with *Dasypus sexcinctus* rather than with *Orycteropus*.

Putting aside Humphry's statement with regard to *Orycteropus* which may have referred to an anomalous specimen, we have no case in which both *fabellae* occur in the Edentates. Even if Macalister's statement as to *Cyclothurus* be correct, we have only one case in which both *cyamella* and lateral *fabella* are present, and only two cases in which lateral *fabellae* have been recorded at all. There are two cases, *Dasypus* and *Chlamydophorus*, in which neither *fabellae* nor *cyamella* appear.

Unfortunately we have been able to examine relatively few moist knee-joints of the Edentates, and have had to trust largely to other investigators and mounted specimens. This is especially undesirable in the case of *lunulae*. We know, however, that they certainly exist in the Edentates, for example in *Megatherium cuvieri*, and in *Bradypus sexcinctus*, which have anterior *lunulae*, and in *Prodontes gigas* which has a mesial posterior *lunula*. We also think it safe to say that the specimen of *Orycteropus* examined by us (there were alas! no sesamoids *in situ*) had purely cartilaginous semi-lunars, i.e. no *lunulae*.

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* The mounted specimen of *Orycteropus capensis* in the Museum of the Royal College of Surgeons has what seems to us a *cyamella* or parafibular sesamoid, but it is mounted on top of the external condyle! In the mounted specimen of *Manis aurita* the *cyamella* or parafibular sesamoid rests in what we think a much more natural position, i.e. between lateral condyle and head of fibula. It has been slightly separated from the latter for the sake of photography: see our Plate XXV, Fig. 67.

† "Anatomy of *Chlamydophorus truncatus* with Notes on the structure of other species of *Edentata*," *Trans. Royal Irish Academy*, Vol. xxv. p. 219.

‡ *Loc. cit.* p. 267.

§ We have examined two specimens of *Chlamydophorus* and find no *fabellae* or *cyamella*. The tibia and fibula are distally fused, and the latter is the more important member.

The typical Edentate may be said to be characterised by a large *cyamella* with probably one or more *lunulae*. The mesial *fabella* has practically no existence for this order, and in the few cases where the lateral *fabella* appears, it seems interchangeable with the *cyamella*. There is one group, however, *Dasypodidae* in which neither *cyamella* nor *fabellae* appear. The order of Edentates therefore *from our present standpoint* contains two fundamental groups one of which consists of species with non-sesamoidal knee-joint and the other of species with a sesamoidal knee-joint. The characteristic of the latter is the absence of the mesial *fabella* and the coalescence of lateral *fabella* and *cyamella* to form a large sesamoid which may act as an articulating link between the femur and one or other of the lower members of the limb.

(17) *Marsupials.*

It will be clear to the reader that the views expressed above on the affinities of genera, and orders based on the changes in the sesamoids of the knee-joint must receive strong confirmation, or failing it the *coup de grâce*, when we come to the Marsupials.

Historically we find the same vagueness as to the knee-joint sesamoids as in the Edentates. Meckel talks about the sesamoid of the kangaroo as if the kangaroo presented an "external fabella" only, and he makes a similar statement as to the opossum. Before Meckel Blumenbach had already noticed the external sesamoid in the *Didelphia* generally. Other fairly early notices of the external sesamoid are Pandir and d'Alton in *Didelphis cancrivora*, *Halmaturus elegans* and *H. giganteus* (Meckel also noticed it in *Halmaturus*), Cuvier and Laurillard in *Phalangista carifrons*, and Owen in *Myrmecobius* and some other marsupials. Owen describes the sesamoid as above and behind the external condyle of the femur*.

Gruber while still speaking of the lateral sesamoid of the Marsupials, as if it were directly comparable with the external *fabella* in other orders, gives useful information on its muscular relations. In *Didelphis philander* he tells us it is in the tendon of *gastrocnemius externus*, but articulates with the head of the fibula. The same statement applies to the sesamoid in *Dasyurus viverrinus*. Again in *Phalangista vulpina*, the external sesamoid articulates with the *capitulum fibulae* and is united to the fibula "durch eine schlaffe Gelenkkapsel und durch ein starkes Ligament." It is "fiddle-shaped" and with its thicker upper end the tendon of origin of *gastrocnemius externus* is united ("verwachsen"). In these three genera the external ossicle has no relation to the knee capsule and *popliteus* does not spring from the external condyle of the femur, but from the knee capsule and the *capitulum fibulae*†. None of the above has any internal *fabella*. These three species give very typical marsupial sesamoidal systems. They are cases really in which *fabella* and *cyamella* have coalesced and we do not believe it possible to speak of merely the "lateral" *fabella* existing. The remaining two cases, if Gruber has interpreted them rightly, seem to us more or less aberrant variants of the main marsupial type. They are:

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* *Anatomy of Vertebrates*, Vol. II. p. 358.

† *Loc. cit.* p. 59.

Hypsiprymnus, which has no mesial *fabella*, but (according to G.) a large lateral *fabella* articulating with external condyle*, and no sesamoid in the *popliteus*; and:

Halmaturus where (according to G.) *both fabellae* exist; the lateral articulates with external condyle and is united to tendon of *gastrocnemius*, but it had also a short ligament to the external semilunar. It was "hornformig."

We failed to find a mesial *fabella* in two specimens of *Halmaturus* (sp. ?). The species of *Halmaturus* is also not stated by Gruber.

According to Meckel *Halmaturus* (sp. ?) has only the lateral *fabella* and the same statement is made by Pandir and d'Alton for the species *H. elegans* and *H. giganteus*.

The only other record of a mesial *fabella* in the marsupials that we have come across is due to Windle and Parsons†, discussing the anatomy of *Macropus rufus*. They state that the inner head of *gastrocnemius* had also in the older specimen a *fabella* of much smaller size than that of the outer head and differently situated. "This *fabella* lies below the origin of the muscle from the back of the condyle of the femur and between the muscular fibres and that bone upon which therefore it plays."

We have examined a considerable number of mounted specimens of *Macropus*, the lateral sesamoid was almost invariably preserved but we have failed in any case to find a mesial orthosesamoid preserved‡. It is possible that the articulator in all these cases overlooked the smaller mesial *fabella*, but it is equally conceivable that the mesial *fabella* in Windle and Parsons' case was a hemisesamoid§.

Before discussing further other contributions to our knowledge of the knee-joint in the Marsupials, we wish to draw the attention of the reader to Plate XXIX, Fig. 78. The photograph on the right exhibits the lower limb bones of *Phascolomys*, the wombat. In this specimen there are no sesamoids at all, the large lateral sesamoid is seen as a fibular crest and is fused to the bone. The femur articulates with both tibia and fibula, and the head of the fibula comes in contact with the femur above the lateral condyle where the lateral *fabella* is often placed by the articulator. The limb to the left of the plate is that of *Sarcophilus*, the Tasmanian Devil. Here again the femur articulates with both tibia and fibula. The fibula has a parafibula precisely like that of *Phascolomys*. The summit of the fibula touches the femur above the lateral condyle, and there may even be a pit (as in the sea-otter; see our Plate XIX, Fig. 40) for its reception‖. The reader may say: "But this is the large external *fabella* of the marsupial myologists." It is and it is not; it really consists of two sesamoids, the lateral *fabella* and the *cyamella*; *they are in this case fused together and fused to the head of the fibula.*

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* Confirmed by us on an articulated specimen of *Hypsiprymnus murinus*.

† *Journal of Anatomy and Physiology*, 1897, p. 128.

‡ *Macropus rufus*, *Macropus* (sp.), *Macropus agilis*, *Macropus major*, *Macropus bennettii*, etc.

§ At the same time we note that without finding a mesial *fabella*, we have found a cartilaginous thickening—hardly a hemisesamoid—in a specimen of *Macropus agilis* and in one of *Dendrolagus*, the tree kangaroo.

‖ As for example in the mounted specimen in the British Museum (Natural History).

Plate XXIX, Fig. 79, gives a second wombat; here the big sesamoid is not fused to the head of the fibula, but it nevertheless consists of the associated *lateral fabella* and the *cyamella* fused together, a true parafibula. The limb has had to be extended to separate the sesamoid from articulating on the femur. The reader should now examine our drawing after Pfitzner in Plate V, Fig. 13, of this memoir, where the muscular attachments have been entirely removed; he will (as a careful study will show him in the present plates) be able to detect the two portions of the associated bone, which become respectively the lateral *fabella* and *cyamella*. These two portions of the great marsupial sesamoid of the knee-joint are also quite distinguishable in *Phalangista*. See our Plate XXX, Fig. 80.

While the hypothesis that lateral *fabella* and *cyamella* are the product of the breakdown of the parafibula finds much support from the fact that specimens occur in which these sesamoids are actually fused together and to the fibula*, we have to consider how far this hypothesis fits the myological facts and tends to throw light on Gruber's description of the lateral *fabella* in man as a muscular "Knotenpunkt." We have above all to ask whether the Marsupials themselves provide evidence in favour of this break-up of a parafibula. One of the most noteworthy facts in this respect is the occurrence in certain marsupials of a hemisesamoidal *cyamella*, this articulates on the head of the fibula, and upon this *cyamella* articulates the lateral *fabella*, which in its turn is in contact with the upper part of the condyle of the femur.

A specimen of *Macropus* (sp. ?) sent to us from Australia shows a lateral *fabella* —an orthosesamoid—and a hemisesamoid *cyamella*. The specimen consisted only of the lateral branch of the *gastrocnemius* with its orthosesamoid, the hemisesamoidal *cyamella* and the external semilunar cartilage all attached, these for the left hind limb. It was thus not possible to draw the knee-joint showing these in their natural position. It is not, however, difficult to understand their relations to other structures in the knee-joint, if a comparison be made between these drawings and those of other members of the *Marsupialia*. See Plate XXXIII, Figs. 83 *a* and 83 *b*.

In a museum specimen of *Macropus agilis* we found also this hemisesamoidal *cyamella*, while the lateral *fabella* was a large orthosesamoid. In the mesial head of *gastrocnemius* there was a cartilaginous nodule, possibly a hemisesamoid.

In another mounted specimen of *Macropus rufus* the large lateral sesamoid was simply wired on to the femur, a process which completely fails to indicate the sesamoid system as a link between femur and *capitulum fibulae*. Our Plate XXXIV, Figs. 87 and 88, shows museum specimens of *Macropus bennettii* and *Perameles lagotis* in which this sesamoid is simply pinned on to the femur†. Our Plate XXXV, Fig. 90, gives what appears to us to be the position of this sesamoid in Bennett's Wallaby; it has very clearly no relation to the position as indicated in Figs. 87 and 88.

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* We have never in examining several hundred knee-joints found a case in which the sesamoids were fused to the femur, and the only recorded case of ankylosis that we have met with is that reported by Gruber in a specimen of *Myogale*.

† We have also found the parafibular sesamoid treated in this manner in the case of *Dendrolagus ursinus*, where the sesamoid is generally similar to that of *Macropus bennettii*, and again in *Macropus major*.

But a preparation in the Museum of the Royal College of Surgeons* shows far more clearly the whole arrangement of a knee-joint of this character. We owe photographs of it in anterior and lateral aspects to Mr S. Steward (see our Plate XXXIV, Figs. 89 *a* and 89 *b*). They show the sesamoid mounted vertically on the top of the fibula and connected proximally by a tendon to the femur above the lateral condyle. The sesamoid itself is a true parafibula and does not articulate with the femur at all, as is well indicated by the anterior aspect†. In the cases of *Bettongia gaimardi*, *Hypsiprymnus murinus*, and *Myrmecobius fasciatus*, we think there is little doubt that we are dealing with a parafibular sesamoid and not with a simple lateral *fabella*.

Windle and Parsons‡, who have treated at length of the anatomy of *Macropus rufus*, state that

> the tendon of the *popliteus* contains a very strong fibro-cartilaginous *fabella*, which is placed above the head of the fibula to which it is attached, and on which it moves freely. It is with this *fabella* that the large gastrocnemic *fabella*, to be more fully described in another section, articulates.

And again:

> The outer head of the *gastrocnemius* possesses a remarkably large *fabella* already mentioned as articulating with that of the *popliteus*. This was crescentic in shape [see our Plate XXXV, Fig. 90] and in the older specimen measured 2·5 cms. from one corner to the other.

To the muscular attachments as noted by our authors we shall return later. We are here only concerned with making the point that the *cyamella* portion of the associated femoro-fibula sesamoidal link of the Marsupials may in certain species have degenerated into a cartilaginous§ mass—a hemisesamoid. In cases where this hemisesamoidal *cyamella* disappears entirely the whole purpose of the *fabella-cyamella* system is lost to sight, and we are provided with a detached sesamoid on the lateral condyle associated with a system of muscular attachments which formerly were associated with the *capitulum fibulae*.

It seems to us that in the *Marsupialia* there has been written the complete history of the lateral sesamoids of the knee-joint. We have:

(i) No sesamoids at all but a fibular crest, a continuous part of the fibula (some specimens of Wallaby).

(ii) The parafibula is still fused with the fibula but shows signs of splitting into two parts, *fabella* and *cyamella* (certain specimens of Tasmanian Devil).

(iii) The parafibula separates off as a large lateral sesamoid being an articulating link between femur and fibula. The two parts *fabella* and *cyamella* are still united (this is the general rule in the wombat).

(iv) The large lateral sesamoid breaks up into two components, the *fabella* and the *cyamella* (this is the case in *Didelphys*), or:

(v) The *cyamella* becomes a mere hemisesamoid (*Macropus rufus*), or:

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* See note †, p. 69.

† This parafibular sesamoid is not shown in the figured skeleton of the wallaby on p. 130 of Vol. x. of the *Cambridge Natural History*, nor is it referred to in the text; even with Galen of such bones "non est necessarium hoc opere pertractare"!

‡ "On the anatomy of *Macropus rufus*," *Journal of Anatomy and Physiology*, 1897, p. 123 and p. 128.

§ We much doubt its being "fibro-cartilaginous" as Windle and Parsons state. A section of the *cyamella* in *Macropus* should be examined as soon as possible microscopically.

(vi) The *cyamella* disappears entirely or almost entirely, being merely represented by a thickening of the popliteal tendon at the position where definite ossification occurs; noted in some cases of *Didelphys.*

We have already illustrated (i) and (ii) from individual specimens of the wombat and the Tasmanian Devil. (iii) is the more general case of both Tasmanian Devil and wombat. It is also the case of *Dasyurus macrourus, Dasyurus ursinus, Perameles nasuta* and in some instances of *Phalangista vulpina**.

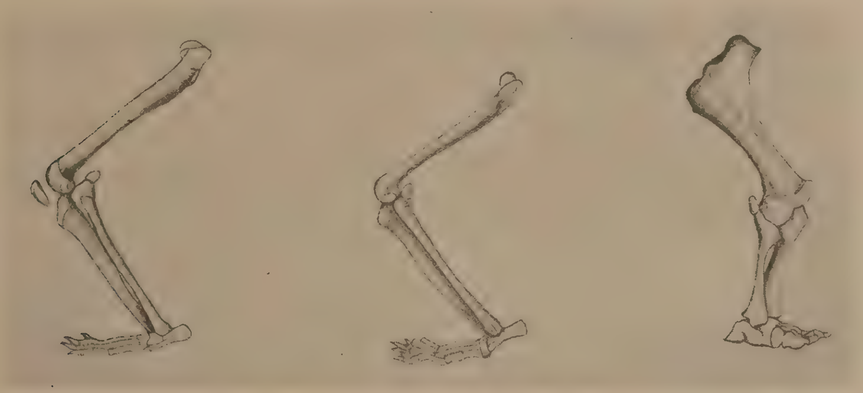
Didelphys virginiana is typical for (iv). Our sketch, Plate XXXIII, Fig. 84, shows the relative position of *fabella* and *cyamella*—they form together when the cut ends of *gastrocnemius* are reunited an articulating link between the head of the fibula and the external condyle. The reader must remember that in the natural position the limb is much more flexed than in the sketch.

(v) Our drawing, Plate XXXIII, Figs. 83 *a* and 83 *b*, indicates in *Macropus* the *fabella* with hemisesamoidal *cyamella.*

Our drawings of *Phalangista vulpina* and *Phascolarctus* indicate the nature of the lateral side of the knee-joint when there is a single parafibular sesamoid which has often been described as a *fabella lateralis* (see Plate XXXIII, Figs. 85 and 86).

In mounted specimens of *Bettongia gaimardi, Hypsiprymnus murinus, Peragalea lagotis*†, *Myrmecobius fasciatus,* we found only a sesamoid attached to the lateral condyle.

Fossil Marsupials showing Parafibulae.



Prothylacinus patagonicus *Cladosictis lustratus*
From the Santa Cruz Beds, after Sinclair

Diprotodon australis
after Shaw and Parker

The fossil *Diprotodon australis*‡ belongs apparently to class (iii), and shows according to Professor Stirling's restoration a large parafibula which would only come in contact with the femur on extreme flexure. This figure throws much light on the position of the large lateral sesamoid in the Tasmanian Devil (see our Plate XXXIV, Figs. 89*a* and 89*b*) and in *Halmaturus* (see our Plate XXXV, Fig. 90).

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* Our photograph, Plate XXXIII, Fig. 85, shows the combined sesamoid in *Phalangista.*

† In specimens of *Peragalea lagotis* and *P. leucura* the fibula did not articulate with femur, there was no ossification in the popliteal tendon, but the lateral *fabella* was present.

‡ See Parker and Haswell, Vol. II. p. 602, Fig. 1229. The fossil Patagonian Marsupials reconstructed by Sinclair show fibular crests (or parafibulae?). See his plates of *Cladosictis lustratus* and *Prothylacinus patagonicus.* He gives no details, however, on this point. He does say that the patella is ossified in the latter. See *Proc. American Phil. Soc.* Vol. XLIV. pp. 73—81, Philadelphia, 1905.

In *Pseudochirus peregrinus*, one of the phalangers, the lateral condyle of the femur articulates with the fibula and both lateral *fabella* and *cyamella* are present. The fibula was prolonged upwards and posteriorly into a wing on the top of which the lateral *fabella* was found. The *cyamella* is a small nodule or inner notch of fibula. The arrangement is somewhat similar to that of *Didelphys*.

If the hypothesis developed in this paper be correct, namely that the lateral *fabella* and *cyamella* are vestiges of the break-up for the parafibula of an early mammalian evolutionary stage, we ought to find the lateral head of *gastrocnemius*, in whole or part, and the tendon of *popliteus* transferred to the *capitulum fibulae*. We shall turn shortly to the myology of the Marsupials and inquire whether there is any support for such a view.

One of the noteworthy points of the Marsupials and Monotremes is the apparent absence of *lunulae* which are so definitely present in many reptilian forms. We have failed to find them in *Ornithorhynchus*, or in the koala, wombat and a variety of kangaroos. The alternatives before us are: to suppose that both Monotremes and Marsupials have lost original *lunulae*, although they occur regularly or at least as anomalies in many placentals, or to suppose both to have originated in a reptilian form possessing a fibular crest or a parafibula, but no *lunulae*. A similar problem arises in the case of the Ungulates; we must suppose them to have completely lost all sesamoids of the knee-joint, and so thoroughly that they do not even appear as in man as anomalies, or we must conceive them descended from an ultimate form which has never possessed *parafibula* or *lunulae*.

(18) *On changes in the muscular attachments of the knee-joint.*

If we look upon the lateral *fabella* and the *cyamella* in Man as vestiges of an earlier structure which has now disappeared, it becomes of importance to consider the evolutionary history of the muscles attached to these sesamoids. Does it indicate a transition of their attachments from one bone to a second which is compatible with a transfer of the sesamoids from one bone of the lower limb to a second? We venture to think it does, and shall endeavour to place before the reader in this section our reasons for believing that the transfer of muscular attachments from the head of the fibula to the distal epiphysis of the femur has been accompanied by a transfer of the remnants of the parafibula to the lateral condyle of the femur.

The muscles with which we are principally concerned are *M. gastrocnemius* (in particular the lateral branch), *M. popliteus* and *M. plantaris*. Gruber has gone so far as to assert that the lateral *fabella* serves a useful purpose as a "Knotenpunkt" directing on the posterior surface of the lateral condyle the movements of *gastrocnemius externus*, *plantaris*, *semimembranosus* and occasionally *M. popliteus biceps*, when this anomalous supernumerary head of *popliteus* is present. Without accepting this interpretation of "usefulness" in a vestigial structure, we would suggest that the "Knotenpunkt" nature of the lateral *fabella* is a phenomenon to be accounted for. We must seek for an important structure to which these muscles could have been originally attached, and which in a pre-vestigial stage had a use value*. The supernumerary head of *popliteus* arising in the *fabella*, connects the lateral *fabella* at once with the *cyamella* in the principal head of *popliteus* as possible parts of the same original structure. The next point is to consider what changes have taken place in the attachment of *popliteus*. There is no doubt that in the course of evolution *popliteus* has migrated from the head of the fibula to the lateral face of the external condyle. Take the *cyamella* with the popliteal tendon attached still both to the condyle and to this sesamoid and place it at the head of the fibula; place the lateral *fabella* on top of the *cyamella*; fuse them together and we have by no means a bad representation of the muscular attachments of the highly flexed marsupial knee-joint and their relations to the parafibular sesamoid. Fuse this parafibula to the head of the fibula and we have a rough representation of the muscles of the knee-joint of the Monotremes.

Let us examine first the Monotremes. *Popliteus* in *Echidna* arises from the extremity of the process at the top of fibula instead of from the external condyle. *Gastrocnemius* is a slender and delicate muscle arising from the internal condyle; this is really the internal head, and the external head appears to be replaced by *Soleus* which "arises by tendinous fibres from the posterior and outer margin of the singular process at the summit of the fibula." This is Mivart's account† of these muscles; he does not refer to *plantaris*.

Manners-Smith has dealt with *Ornithorhynchus*‡, and describes the knee-joint musculature as follows:

He tells us that *gastrocnemius* is a large muscle arising by two distinct heads, a larger from the fibular crest and a smaller from "the lower end of the femur." It does not fuse with the *soleus*. The femoral head, he states, is supplied by the external popliteal. *Soleus* arises from the fibular crest and from the shaft of the fibula. A *few* fibres only arise from the tibia. Manners-Smith contradicts Owen's assertion that a large proportion of the fibres arise from the tibia and asserts that it is certainly a mistake. He gives no information about *popliteus* or *plantaris*. Our drawing (Plate XX, Fig. 42) shows the external head of *gastrocnemius* having no attachment to the external condyle and the internal head attached to the internal condyle.

In Reptiles *popliteus* arises from the fibula§, probably also from a groove on the external condyle and when it exists from the parafibular sesamoid||. According to

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* As we have previously remarked we cannot consider a structure which has only an occasional and anomalous occurrence to have real "use" value; it can only be degenerating, i.e. vestigial.

† "Anatomy of *Echidna hystrix*," *Trans. Linnean Society, London*, 1866, p. 394.

‡ "Anatomy of *Ornithorhynchus*," *Proc. Zoological Society, London*, 1894, p. 707.

§ Mivart, "Myology of *Iguana tuberculata*," *Proc. Zoological Society, London*, 1867, p. 796. *Popliteus* arises from tibial aspect of head of fibula.

|| See our p. 85, and the drawings of *Varanus*, Plate XXIV, Figs. 64 *a* and 64 *b*.

Macalister* *popliteus* in birds may be femoro-tibial or fibulo-tibial in origin, and the origin of *soleus* is also variable. There is of course the possibility that *popliteus* was not in the earlier stage largely fibular in its attachment, but acquired an attachment to the fibula in the marsupials. This appears to be the view of Parsons who writes†:

> In the koalas, the phalanger, the opossum and the Tasmanian devil, the great mobility of the fibula has produced the same effect on the *popliteus* that we noticed in the lemur, the fleshy part acquires an attachment to the fibula, while the tendon is converted into an extra external lateral ligament.

The question arises, however, as to whether the popliteal attachment to the fibula is not the earlier stage and thus the arrangement we find in the lemur would be vestigial. When the parafibula broke up, it is conceivable that *popliteus* carried off with the *cyamella* the whole or a portion of a fibulo-femoral ligament, i.e. it is not the tendon of *popliteus* converted into a ligament, but a ligament which has become the tendon of *popliteus*.

The point has been studied also by Gordon Taylor and W. V. Bonney‡. They take the view that the ultimate origin of the *popliteus* was fibular; that as movement between the tibia and fibula ceased to exist the upper origin of *popliteus* ascended to the external femoral condyles, but that in the lemur where movement between tibia and fibula has reappeared the *popliteus* appears to be descending to its primitive fibular attachment. The lemur problem is a question either of reversion or of vestige. The question of whether the fibula attachment of *popliteus* is the original attachment or an acquired one seems worthy of much more study especially in relation to the origin of the lateral knee-joint sesamoids, in particular to the muscular attachments of the parafibula in Reptiles.

Passing from the Monotremes to the Marsupials it becomes difficult to appreciate the contributions of various writers to the subject, for they invariably speak of the parafibular sesamoid as if it were a large *fabella* in the lateral head of *gastrocnemius*. Thus we find it hard to interpret the following statement of Macalister with regard to the myology of the Marsupials§:

> The *gastrocnemius externus* in the Wombat, Giant Kangaroo, Sarcophilus and Bennett's Kangaroo arises from the sesamoid bone at the back of the external condyle of the femur and is inserted into the tendo Achilles, etc.

It seems to us extremely difficult to speak of the parafibular sesamoid, which may even be fused to the fibular head, in the Wombat and Tasmanian Devil (see our Plate XXIX, Fig. 78) as a sesamoid at the back of the external condyle! The same difficulty occurs in the Wallaby (Bennett's kangaroo, or Halmaturus): see our Plate XXXV, Fig. 90. We are dealing in all these cases with something much more closely allied to fibula than to femur.

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* "On some Points in Bird Myology," *Proc. R. Irish Academy*, Vol. II. 1875—77, p. 57.

† "Joints of Mammals compared with those of Man," *Journal of Anatomy and Physiology*, Vol. XXXIV. p. 313, 1900.

‡ "Homology and Morphology of Popliteus," *Journal of Anatomy and Physiology*, Vol. XXXIX. p. 35.

§ "Myology of the Wombat (*Phascolomys wombata*) and the Tasmanian Devil (*Sarcophilus ursinus*)," *Annals of Natural History*, 1870, p. 19 of our offprint.

Again:

> The *popliteus* in the Wombat and Sarcophilus is very large but thin, arising from the upper third of the back of the fibula, and inserted into the lower two-thirds of the back of the tibia. A few fibres of this muscle in Sarcophilus are attached to the sesamoid bone in the outer head of *gastrocnemius*. This muscle is smaller in the Giant Kangaroo, but in this and *Macropus bennettii* its origin is purely sesamoid*.

These two passages taken together suggest that both in the Great Kangaroo and the Wallaby *gastrocnemius externus* and *popliteus* arise from a *fabella* or sesamoid at the back of the external condyle. They do not suggest that they arise from a parafibular structure, which may be opposed rather laterally than posteriorly to the femur (see our Plate XXXIV, Figs. 89 *a* and 89 *b*), and which is itself united by a stout band to the femur above the external condyle, this band corresponding in the placentals to the tendon of *gastrocnemius externus*.

Macalister's statements about other muscles are clear. He tells us that *gastrocnemius internus* arises from the internal condyle and joins the tendo Achilles... it is larger than the *externus* in the Wombat, but smaller in the Tasmanian Devil and in all species examined was without sesamoid.

Soleus has a fibular small origin in the Wombat, but as usual has no tibial heads. The *soleus* is fibular also in Tasmanian Devil, Opossum, Phalanger and Giant Kangaroo.

The *plantaris* in the Opossum and Perameles is small but separate from the outer condyle to the outer side of the head, but no *plantaris* exists in the Wombat. A distinct small muscle in the Tasmanian Devil passes from the back of the external lateral ligament and from the head of the fibula down the internal side of the calcaneum and into the plantar fascia†.

In a *Macropus sp.* examined by one of the present writers the parafibular structure consisted proximally of an orthosesamoid from which *gastrocnemius externus* arose, this sesamoid articulated on a hemisesamoid which was linked by a tendon to the lateral face of the external condyle and from which *popliteus* arose; this hemisesamoid rested on the *capitulum fibulae. Plantaris* was not identifiable in our specimen. The orthosesamoidal part of this parafibular structure is what is termed by most writers the *gastrocnemial* lateral *fabella*, and the hemisesamoid is what we term the *cyamella* portion of the parafibular structure. *Popliteus* is not attached to the orthosesamoidal part of the structure at all. Interpreted in our own terms we see that this practically agrees, except with regard to *plantaris*, with what Windle and Parsons report of *Macropus rufus*‡:

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* *Loc. cit.* p. 17 of our offprint.

† Macalister, *loc. cit.* p. 19 of our offprint.

‡ *Journal of Anatomy and Physiology*, Vol. XXXII. p. 123, 1897. They say of *plantaris*, that the upper cornu of gastrocnemial *fabella* as well as external condyle give rise to *plantaris* which is thus a double-headed muscle.

> The tendon of the *popliteus* contains a very strong fibro-cartilaginous fabella, which is placed above the head of the fibula to which it is attached, and on which it moves freely. It is with this fabella that the large gastrocnemial fabella articulates.

In another paper* Parsons notes that in the koala, the phalanger, the opossum and the Tasmanian Devil the fleshy part of *popliteus* has acquired an attachment to the fibula while the tendon is converted into an extra external lateral ligament.

According to the views expressed in this paper it may be anticipated that the primitive marsupial would have a fused parafibula, and accordingly the later tendon of *popliteus* would be a femoro-fibular ligament and *popliteus* would arise from the fibula. From this standpoint it is not surprising that on the break-up of the fibular crest certain portions of *popliteus* should still be attached to the fibula rather vestigially than as an acquirement.

We dissected a specimen of Koala (*Phascolarctus cinereus*) and found the parafibular sesamoid articulating with the fibula: see our Plate XXXII, Figs. 82 *a* and 82 *b*. The fleshy portion of *popliteus* was attached to the fibula and the popliteal tendon ran from the antero-proximal corner of fibula to popliteal groove of external condyle. Also tendinous fibres from the fleshy portion on fibula cross the posterior surface of the fibula and mingle with the tendinous fibres of *gastrocnemius*, which run from the sesamoid to the external condyle.

No *plantaris* was discoverable. Young in his paper on the "Muscular Anatomy of the Koala†" does not refer to *popliteus* or *plantaris*, but states that *gastrocnemius* is well developed and arises by two heads in the external of which a *fabella* exists. We again urge that this parafibular sesamoid should not be described as a *fabella*. We think that for the whole genus *Macropus* we ought to consider that we are dealing with a parafibular structure and not a lateral gastrocnemial *fabella*. We have not been able to examine a case of *Petrogale xanthopus*, but Parsons' description seems in accordance with the above interpretation, if we replace his term *fabella* by parafibular sesamoid. Thus he says‡:

> The knee-joint like the hip is never fully extended, the capsule is strengthened by strong lateral ligaments; the external lateral runs downwards and backward from the external condyle to the front of the head of the fibula; its anterior fibres are continuous with the origin *extensor longus digitorum*. The *popliteus* also performs the function of an external lateral ligament, since it is attached to the femur and fabella, and below to the external semilunar cartilage and the head of the fibula. During extreme flexion which is the usual position of the joint, the *fabella* articulates with the head of the fibula.

Judging from the knee-joints of other specimens of *Macropus* with which we are more familiar, we should believe that the parafibular sesamoid was always in contact with the fibula and that in cases of extreme flexure its head may come in contact with the postero-lateral border of the femur. We do not think that like an ordinary *fabella*, it will be found to articulate with the articular surface of the lateral condyle. Turning to the muscular attachments Parsons states:

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* "Joints of Mammals compared with those of Man," *Journal of Anatomy and Physiology*, Vol. XXXIV. p. 313, 1900.

† *Journal of Anatomy and Physiology*, 1882, p. 237.

‡ "On the Anatomy of *Petrogale xanthopus* compared with that of other Kangaroos," *Proceedings Zoological Society, London*, 1899, p. 690.

> The *gastrocnemius* has the usual two heads, the outer of which has three origins: (1) a small head from the outer side of the patella, (2) larger from the same place and separated from the last by the external popliteal nerve, (3) from the large *fabella* over the external condyle and from the external semilunar cartilage. The inner head is normal in origin and has no *fabella* developed in it (p. 207).
>
> The *soleus* is absent unless the origin of the *gastrocnemius* from the semi-lunar cartilage represents it. Meckel also describes it as wanting.
>
> *Plantaris* comes from the external *fabella**.
>
> *Popliteus* arises from the external condyle, partly from in front of the groove, and partly from the groove itself, which is deep and narrow and not adapted for the tendon to lie in†. The muscle also has an origin from the external semi-lunar cartilage and from the head of the fibula.

We see in this typical description of a marsupial knee-joint, *gastrocnemius*, *popliteus* and *plantaris* all associated with the parafibular sesamoid. We see the muscles which largely arise from the fibular crest in the Monotremes now attached to the parafibular sesamoid, and the fragments of the parafibula will be carried with them as *fabella* and *cyamella* to their ultimate tendons of insertion on the lateral femoral condyle. We begin to see now why the early human anatomists associated the lateral *fabella* with numerous muscles, why *popliteus* (with its anomalous head) passes to *fabella* as well as to *cyamella*; how Gruber could confuse these two sesamoids, and why he emphasised so strongly the "Knotenpunkt" character of the lateral *fabella*.

While *Macropus* seems to us to represent a later evolutionary stage of the parafibular sesamoid than *Phascolomys*, for in the Kangaroos we have various stages of disruption of the parafibula, while in the Wombat it may still be fused, the Phalangers form a more or less intermediate stage. They have a parafibular sesamoid of much the same form as the wombat's—quite different from that of the wallaby—and its form is seen to be clearly that of a fibular crest: see our Plate XXXIII, Fig. 85.

As Cunningham has shewn, *gastrocnemius* in *Phalangista maculata* springs from the posterior aspect of the fibula in its upper two-thirds, and *plantaris* from the parafibular sesamoid. Cunningham suggests that *gastrocnemius* is a compound muscle containing *soleus*‡. The musculature is much the same as in the Koala (*Phascolarctus cinereus*), except that in the latter we did not identify *plantaris*§, which is also said not to exist in the Wombat.

In *Perameles nasuta* we have the parafibular sesamoid, but the *Peramelidae* are transitional to the *Didelphyidae*. Parsons has pointed‖ out that "the popliteus tendon instead of being converted into an extra lateral ligament is continuous with its fleshy belly as usual and patella is ossified*." According to Macalister† the *plantaris* in *Perameles* as in *Didelphys* is small and arises from the outer condyle.

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* That is the parafibular sesamoid.

† Any marked popliteal sulcus has disappeared in *Macropus*, see our drawing of the Wallaby, Plate XXXV, Fig. 90.

‡ *Challenger Report*, Vol. v. p. 40.

§ In the Koala there is a collatero-fibular ligament—the ultimate popliteal tendon connecting the parafibular sesamoid with the lateral condyle of the femur.

‖ *Journal of Anatomy and Physiology*, Vol. XXXIV. p. 313, 1900.

Of the *Dasyuridae* Cunningham has dealt with *Thylacinus cynocephalus*: he states that *gastrocnemius* arises by two very large and powerful heads: (1) The outer head which contains the *soleus* is much the larger of the two and it arises by two parts, (*a*) by a fleshy process fixed to a large sesamoid bone placed upon the posterior aspect of the head of the fibula—clearly our parafibular sesamoid, and from a powerful ligament which binds the upper part of this bone to the back of the external condyle of the femur, (*b*) by a tendinous slip attached to the outer aspect of the external condyle of the femur. (2) The inner head springs not only from the back of the inner condyle but also from the whole breadth of the popliteal surface at the same level. *Plantaris* in *Thylacinus* arises in common with the outer head of *gastrocnemius* and remains fused with its under surface for a considerable distance.

We have already noted that in *Dasyurus macrourus* and *D. ursinus* the sesamoid is parafibular (see our p. 71). MacCormick‡ has studied the myology of the limbs of *D. viverrinus*. He states that the outer head of *gastrocnemius* "arises directly from the sesamoid bone over the upper end of the fibula, and indirectly by two strong ligaments which bind this bone to the femur, one being attached to the outer border of the popliteal space, and the other passing over the femur to be attached to the upper border of the patella§ and to the outer part of the *vastus externus* tendon." He does not refer to *popliteus* and *plantaris*.

Didelphys is the last marsupial to which we shall refer. It represents the later stage of the break-up of the parafibula. *Gastrocnemius externus* arises from external condyle and contains a sesamoid—the lateral *fabella*. *Popliteus* follows the course of this muscle in higher mammals, arising from a groove in the lateral face of the external condyle, and contains a *cyamella*. We found no association between *popliteus* and the gastrocnemial *fabella*. But the *cyamella* of the Opossum is wedged between the under surface of the lateral condyle and the head of the fibula (see our Plate XXXIII, Fig. 85), and when the *gastrocnemius* is replaced the *fabella* lies on the external condyle immediately above the *cyamella*. According to Parsons‖, however, the fleshy part of *popliteus* in the Opossum acquires an attachment to the fibula, while the tendon is converted into an extra lateral ligament. This did not seem to be the case in our specimen, the tendon of *popliteus* passed to the *cyamella*, which indeed might be looked upon as a parafibula, but unless that sesamoid was fused the tendon could hardly be treated as an extra lateral ligament in our case. We have already seen that the fusing* of the parafibular sesamoids is a possibility in the Marsupials, rare as it appears to be in the higher Mammals†. It is possible that in certain individuals, or even in one or other species of opossum the *cyamella* may as a vestige be fused to the fibula, and so the popliteal tendon become an extra lateral ligament.

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* It is not ossified in Kangaroos and Wallabies and Opossums, although a small bony element has been reported in certain cases.

† *Annals of Natural History*, 1870, p. 17.

‡ *Journal of Anatomy and Physiology*, Vol. XXI. p. 213, 1887.

§ The reader must remember that the patella is cartilaginous in all Marsupials but *Perameles*, although the existence in certain cases of a small ossified kernel has been asserted. The attachment of the fibular crest to the patella in the case of Platypus may also be borne in mind here.

‖ *Journal of Anatomy and Physiology*, Vol. XXXIV. p. 313, 1900.

Plantaris arises in *Didelphys* from the lateral femoral condyle‡.

It will be seen from the above that *Didelphys*, as far as the sesamoids of the knee-joint are concerned, is among the most advanced of the Marsupials. It stands at the opposite extreme to the Tasmanian Devil with its fused parafibula forming a fibular crest. The range marks the transfer of the *gastrocnemius, popliteus* and *plantaris* from fibula to femur and with them pass both lateral *fabella* and *cyamella* to the lateral femoral condyle.

(19) *Monotremes.*

We now come to the Monotremes and have to bear in mind the fundamental differences we have noted between the *Ornithodelphia* and the *Monodelphia*, in particular the existence of the parafibula, and the rearrangement of the muscular insertions of the posterior aspect of the knee-joint. We turn first to *Ornithorhynchus* (Platypus). Plate XX, Figs. 43 *a* and 43 *b* provide drawings of the femur and distal portions of tibia and fibula. The extraordinary development of the process at the distal end of the fibula will be at once noticed. From this fibular crest (see our Plate XX, Fig. 42) arises the lateral head of *gastrocnemius, plantaris* and *popliteus*. The patella is also attached to this expanded head of the fibula. This is well shown in the prepared specimen in the Museum of the Royal College of Surgeons. The internal head of *gastrocnemius* is attached above the internal condyle of the femur. There are no *fabellae*§, no *cyamella*, and what is more remarkable no *lunulae* (i.e. because the latter are very conspicuous in the Reptiles). Thus platypus verifies what we have observed in the Marsupials: namely that, with the appearance of the fibular crest, there is associated a disappearance of lateral *fabella* and *cyamella*. Accordingly we see in the Monotremes the three muscular attachments which are associated with the lateral *fabella* in Man (see our Part I, p. 29); those of the external head of *gastrocnemius*, of *popliteus* and of *plantaris*, are now associated with the fibular crest. Manners-Smith tells us that‖ *soleus* also arises from the expanded head of the fibula, but partly too from the shaft of the same bone.

By the kindness of Sir Arthur Keith one of us was able to dissect the knee-joint of *Echidna*. There were no signs of any *fabellae*. The popliteal muscle followed much the same course as that shown in the drawing of *Didelphys*, but it lacked any *cyamella* where it passed over the head of the fibula; it arises as in *Ornithorhynchus* from the fibular crest and not from the external condyle of the femur. The expansion of the fibula is not quite so marked as in *Ornithorhynchus*, but from it arises not only *popliteus*, but the larger or external head of *gastrocnemius*. The internal head is much smaller and arises from the internal condyle*.

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* We must not be understood as suggesting that this "fusing" is something which may occur anomalously as in an adult individual; it is specific in the case of the two parts of the parafibula, and vestigial when the parafibula is ankylosed with the fibula.

† See our p. 69, first footnote.

‡ This was so in our specimen, and Macalister says so also: see *Annals of Natural History*, 1870, p. 17.

§ Meckel, *loc. cit.* pp. 634—635, had already noticed the absence of the *fabellae* in Platypus ("Schnabelthier"). Gruber has not investigated the Monotremes.

‖ "Anatomy of Ornithorhynchus," *Proc. Zool. Soc. London*, 1894, p. 707. He also notes the parafibular origin of *gastrocnemius externus*, but says nothing of *popliteus* or *plantaris*.

(20) *Centre of Ossification of Fibular Crest in Monotremes.*

In order to grasp how the fibular crest can be separated from the fibula and ultimately be found disintegrated as vestigial sesamoids attached to *gastrocnemius*, *popliteus* and *plantaris*, it is of some importance to determine whether this process at the head of the fibula has a separate centre of ossification.

Parker and Haswell† appear to have no doubt on the matter; writing of the Monotremes they say:

> The fibula has at its proximal end a remarkable compressed process which ossifies from a separate centre and greatly resembles the olecranon of the ulna.

Through the great kindness of Dr Wm. Colin Mackenzie of the Australian Institute of Anatomical Research, Melbourne, we were able to obtain sections of the fibula both of an embryonic and a young platypus. He also sent us the section of the parafibular sesamoid of a young wombat which had just left the pouch. Fig. A, on p. 81, indicates the bone of the young platypus set against that of an adult platypus to give the relative sizes. The length of the former animal from tip of bill to cloacal sphincter was 31 cms. as against the similar length of a fully developed adult of 44 cms. The length of the embryonic platypus was 13 cms. Fig. B shows the position of the sections Dr Mackenzie made of the embryonal and young platypus.

Taking the section A of the embryo (see our Plate XXXVII, Fig. 96), we have periosteum at the proximal end of the fibular process (top of plate), then follows a small area staining yellow and suggesting ossification, then an area of cartilage with every appearance of ossification starting, and then cartilage again. This certainly seems to accord with a centre of ossification in this fibular process or crest. In the young platypus in the corresponding section A we found no cartilage at all but bone covering the areas where in the embryo we had found cartilage and ossification taking place. It was therefore probably not young enough to show an intermediate partly ossified stage. On the other hand the section towards the top of the crest (Plate XXXVII, Fig. 95) shows fairly numerous Haversian canals which become less frequent or cease altogether as we pass down the section, to become frequent again and in a different direction as we reach the shaft. Their arrangement seems to us not inconsistent with a separate centre of ossification for the fibular crest.

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* Mivart ("Anatomy of *Echidna hystrix*," *Trans. Linnean Soc.* 1866, p. 394) mentions only what appears to be the inner head of *gastrocnemius*, and probably our outer head is his *soleus*, which like his *popliteus* arises from the process at the top of the fibula.

† *A Text-book of Zoology*, Vol. II. p. 489, London, 1897. The comparison of the olecranon with the tibial crest seems more reasonable, the fibular crest should be homologous with a radial rather than an ulnar process. The fibular crest of the Monotremes or that of certain Marsupials has little general resemblance to the olecranon, while the tibial crest in birds (*Colymbus*) or the tibia plus patella (as in *Hesperornis*) is very similar to the olecranon in appearance.

Our view differs from that of Dr Mackenzie and Mr W. Owen, histologist to the Australian Institute. They speak of section A of the embryo as if it were wholly cartilaginous. It seems to us as if a portion of this superstructure of the fibula does show ossification starting (Plate XXXVII, Fig. 96). The articular process of fibula, section B of Fig. B below, has a distinct centre of ossification in the embryo. Further the section at C also shows ossification and Dr Mackenzie tells us that there is one at the distal end (section not forwarded). There would thus appear to be *four* centres of ossification, of which only three are to be found in the higher Mammals. The suggestion is that the fourth centre of ossification is at the basis of the parafibular sesamoid of the Marsupials, or the later *cyamella* and lateral *fabella*.

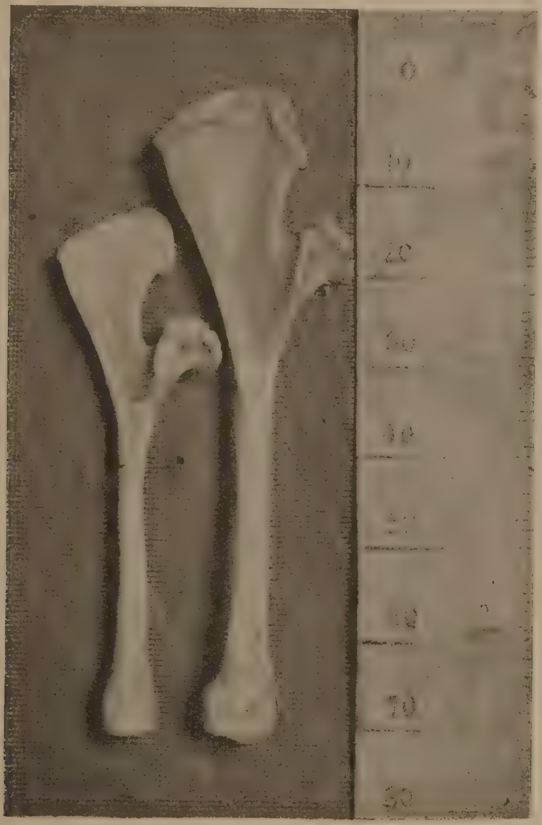

Fig. A.

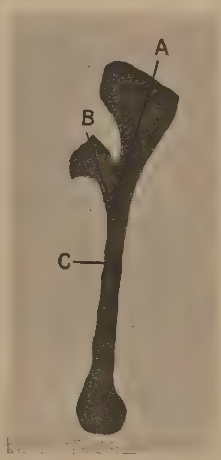

Fig. B.

If the above view be correct that the Mammals with lateral sesamoids of the knee-joint are descended from a primitive mammalian form with a crested fibula, we should anticipate that still lower in the evolutionary scale, e.g. in the *Aves* or *Reptilia*, no lateral *fabella* or *cyamella* will be discoverable. It may be objected that the present hypothesis provides no account of the origin of the mesial *fabella*. That is quite true, but it has appeared over and over again in the course of our investigation that, whatever the origin of the mesial *fabella*, that origin must be differentiated from that of the lateral *fabella*. Not only has the mesial come later in most orders and disappeared in the higher types much sooner than the lateral, but it is far less significant in size and far rarer as an anomaly. Further, while the lateral head of *gastrocnemius* in the earlier forms is attached not to the lateral condyle but to the head of the fibula, the mesial head retains its association with the internal condyle even in the Monotremes. It would demand much further study than we have been able at present to give to the mesial *fabella* to trace satisfactorily its origin and the source of its frequently imperfect condition. We would note, however, that if the lateral *fabella* and *cyamella* arise from a crested fibula, one might seek for a similar origin of the mesial *fabella* (and the reputed mesial *cyamella*?) in a like extension of the head of the tibia. Perhaps in this the cnemial crest of the tibia in certain birds—the *Tubinares* and still more the *Pygopodes*—might be borne in mind*. According to Shufeldt it has (like the fibular crest in Platypus) a separate centre of ossification and may be regarded as representing the olecranon of the ulna. Vicq d'Azyr as early as 1774, and he was followed by Owen, considered the patella itself to be homologous with the olecranon†. It is difficult to accept the view of the more modern writers that fibular or tibial crests are only extensions of the upper epiphysis of these bones if we find they have separate centres of ossification. Still less does it help us to be told that the patella is only a sesamoid, unless we hold the view that a sesamoid can be produced by some mechanical process when and wherever it is likely to be of service‡. At any rate if it can be, there seems no reason why we should stop at a sesamoid—the production of which would be at present as inexplicable as that of any new organ, and would require at least an acceptance of Lamarckism to ensure its perpetuation.

Besides the cnemial crest of birds as a vague suggestion§, there is a faint possibility of the transfer of a mesial posterior *lunula*, but we are unable to cite a case of any fibres of the mesial head of *gastrocnemius* being attached to the semilunar. Such cases may, however, exist.

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* See W. P. Pycraft, *Proc. Zool. Soc. London*, 1899, pp. 401 and 1037.

† "Mémoire sur les Rapports qui se trouvent entre les usages et la structure des quatre extrémités dans l'Homme et dans les Quadrupèdes," *Histoire* [*et Memoires*] *de l'Académie Royale des Sciences*, 1774, pp. 254—270, Paris, 1778. Vicq d'Azyr associates tibia with the ulna and fibula with the radius. He does not, however, claim the association of patella and olecranon to have originated with himself, although many later writers have attributed it to him,—"la rotule qui tient lieu d'olécrâne comme plusieurs anatomistes l'ont démontré" is how he writes on pp. 260—261.

‡ "I could imagine if further strength were required a sesamoid would be called into being"—as an anatomist once wrote to one of the present authors.

§ There are evidences that the cnemial crest is not a specialised development reached only in a small group of birds. Thus Shufeldt found it as a vestige—disappearing with growth in the young of *Centrocercus*, and states that in the present state of our knowledge this is incomprehensible, "for in the old and mature birds of any of the Grouse the epicnemial crest is never very prominently produced, nor is it in any of their near kin. As age advances this segment becomes thoroughly confluent with the tibia, and leaves no trace of its early existence." "Osteology of the North American Tetraonidae," *Bulletin of the U.S. Geological Survey*, Vol. VI. p. 344, 1881.

(21) *Birds.*

We have not examined a large number of birds' pelvic limbs, but we have not found in any of the cases we have examined nor in mounted skeletons either *fabellae* or *cyamella*. On the other hand we have found *lunulae*, for example, in *Syrnium stridula* (the Wood Owl) and *Dendrocygna* (the Tree Duck), the latter having in our specimen at least three posterior *lunulae*. The tibia of this bird also possesses a marked cnemial crest (see Plate XXII, Figs. 52, 53 and 54) apparently articulating with a small patella; this crest reaches to the level of the top of the patella. In Divers, Grebes, Albatrosses (see Plate XXII, Figs. 50 and 51), etc., this crest formed from an extension of the middle and internal crests of the tibia becomes a still more emphasised process and can even be as long as the femur itself*.

The homologue to the tibial crest appears to be the olecranon of the ulna†. Owen has noted in certain birds an ossiculum belonging to the ulna which he states is "essentially the separated olecranon of that bone. This detached sesamoid bone is found attached (like the patella of the knee-joint) to the capsular ligament and the tendons of the extensor muscles in many of the *Raptores* and in the Swifts. In the Penguins it is double‡." It would seem more justifiable to compare the cnemial crest of the tibia with the olecranon than the latter with the fibular process of the Monotremes, and not unreasonable to suppose that if the olecranon can give rise to sesamoids, a similar change can take place in the cnemial crest. In *Apteryx australis* there is a semi-cnemial crest surmounted by a cartilaginous patella. It is true that in some birds we know with marked cnemial crests the patella still exists, partly articulating with the femur and partly with the cnemial crest, but in *Colymbus* it is reduced to a "flake-like bone§." The patella, as we have remarked, has been associated with the olecranon by Vicq d'Azyr||. Shufeldt, while associating the olecranon with the cnemial crest, looks upon the patella as not arising from its partial break-up, but treats the patella as a sesamoid.

We have carefully studied the evidence given by Shufeldt¶, but it seems to us quite as capable of interpretation in favour of the patella being originally the part or whole of the cnemial crest, as of both having quite distinct and separate origins. He first cites the great diversity of patellar forms in birds, from its absence in certain species, as *Haemotopus niger*, to the small double almost cartilaginous

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* According to Owen its importance arises from the provision it affords for extensive attachments by way of insertions for the extensors of the tibia and by way of origin to the extensor of metatarsus. Thus the power of the back stroke of the foot is increased: see Todd's *Cyclopaedia of Anatomy and Physiology*, Vol. I. p. 287.

† Coues writes of *Colymbus torquatus* (*loc. cit.* on our p. 88) that the tibial crest exactly resembles the olecranon of the human species (p. 158).

‡ Owen's article *Aves* in Todd's *Cyclopaedia*, Vol. I. p. 286.

§ Of *Colymbus septentrionalis* (Red-throated Diver) we have examined two skeletons, but found no signs of a *patella*, although the semi-lunars were *in situ*.

|| *Histoire de l'Académie Royale des Sciences*, Paris, 1774, p. 261.

¶ "Concerning some of the forms assumed by the Patella in Birds," *Proceedings U.S. National Museum*, Vol. VII. pp. 324—331, Washington, 1886.

patella of *Mergus servator*, to the flake-like patella of *Colymbus*, up to the huge quadrate patella of *Aptenodytes pennantii*. But he does not seem to lay any stress on the fact that where the cnemial crest is large as in *Colymbus* and *Fulmarus rodgersii* the patella is small, and where the patella is large as in *Podiceps* the cnemial crest is relatively small. Yet this result seems all important and easily interpretable on the assumption of the patella arising from a tibial crest. Lastly Shufeldt gives no explanation of the condition in the cormorant *Phalocrocorax bicristatus* of which he writes that it is almost unique; that on the face of it it almost looks as if a patella had developed of a size equal to that of the tibial crest and subsequently the two became thoroughly united and formed one large patella. This suggestion appears to us as an inversion of the real state of affairs. It also seems to be D'Arcy W. Thompson's view[*]. He treats the large patella of *Hesperornis* as homologous with the tibial crest of *Colymbus*. He actually speaks of this crest as a "co-ossified patella." He writes: "The existence of a small additional sesamoid in the knee-joint of *Colymbus* (Owen, *Comp. Anat.* II. p. 83) does not invalidate the homology here adopted of the long 'rotular process of the tibia' with the patella."

If the cnemial crest be identified with the patella, then it seems to us more reasonable to look upon the patella as a released tibial crest, than the tibial crest as a co-ossified patella[†]. It has not yet been suggested that the olecranon is a co-ossified sesamoid. Perhaps one of the chief difficulties in the idea of the tibial crest as a "co-ossified" patella is the large free patella of the cormorant; here the pro- and ecto-cnemial ridges of the tibia are carried right up the anterior face of the patella itself! (See Plate XXXVI, Fig. 93 *b*.) Why should an independent sesamoid have developed these ridges? Unless we accept the view that a sesamoid can always arise where it is a convenience, this leaves us still without an explanation of the origin of either the sesamoid or the patella. We have at any rate to bear in mind the very close association of patella and cnemial crest where they co-exist[‡].

We note also that whereas a true patella, an orthosesamoid, exists in all placental mammals, it is absent in many Marsupials, it is not invariable in Birds and has disappeared when we get down to the Reptiles. Somewhere between the Reptiles and the branchpoint of the Birds a patella had to arise, somewhere between the Reptiles and the branchpoint of the Monotremes a fibular process had to arise[§],

[*] "On the systematic position of *Hesperornis*," *Studies from the Museum of Zoology in University College, Dundee*, Vol. I. p. 108, Dundee, 1890.

[†] In both *Hesperornis* and *Ichthyornis* the tibia has a considerable epicnemial crest, in the former as well as the massive patella, in the latter no patella is figured or referred to; whether none has been found or it is assumed not to exist, we cannot say. See Marsh, "*Odontornithes*," *U. S. Geological Exploration of the 40th Parallel*, Vol. VII. Plate XXXIV, 1880.

[‡] In the fossil *Hesperornis regalis* which we have examined the patella so far accords with Professor D'Arcy Thompson's view, that it has at least a superficial resemblance to a liberated cnemial crest. See also Plate XXXVI, Fig. 92.

[§] An approach to a fibular crest occurs in some birds; thus in the *Cereopsis Goose* (see Plate XXI, Figs. 48 and 49), the head of the fibula rises above the proximal articulating surface of the tibia, and works in a groove of marked character on the posterior face of the lateral condyle. There is also a substantial cnemial crest.

and somewhere between that branchpoint and that of the Marsupials the fibular process had to be replaced by a parafibula, and lastly somewhere between the branchpoint of the Marsupials and the early placental mammals a *cyamella* and a lateral *fabella* had to replace the parafibula. We can of course take the view that a process will disappear without vestiges, if it ceases to be useful, and that a sesamoid will appear whenever and wherever it is likely to be useful*. But on philosophical grounds there is need of a connected account of the evolutionary origin and subsequent history of even the sesamoids of the knee-joint.

(22) *Reptiles.*

The chief feature of the knee-joint sesamoids of the Reptiles consists in the presence usually of a considerable number of *lunulae*. Parker and Haswell† speaking of the young condition of certain Marsupials state that there is an accessory element situated outside the fibula at its proximal end; "this apparently corresponds to a bone known as the parafibula which occurs in some *Lacertilia*." When the *cyamella* has left the popliteal groove and articulates with the head of the fibula, it becomes very difficult to say whether we are speaking of a *cyamella* or a parafibula. In our opinion the parafibula ultimately is divided into two elements; the upper portion becomes associated with the lateral head of *gastrocnemius* and is the lateral *fabella* of the placentals, the lower portion associated with *popliteus* is the *cyamella* proper. Hence when there is no *fabella* as in the Reptiles and Marsupials it seems a more reasonable course to term the single large sesamoid, which articulates with the head of the fibula and usually at the same time with the under surface of the lateral condyle, the parafibula. At the same time *popliteus* in most of these cases arises from the fibula, it may also be united with the semilunar, and it is not always easy to distinguish this form of the *cyamella*, a small parafibula, from a lateral anterior *lunula*. Our drawings, Plate XXIV, Figs. 64 *a* and 64 *b*, show a typical reptilian knee-joint, that of *Varanus niloticus* (Nile monitor). The anterior aspect shows the *cyamella* as a parafibula. The *popliteus* has a tendon in the popliteal groove of the femoral condyle, it is also attached to the superior posterior corner of the fibula, just internal to attachment of the external lateral ligament shown in the drawing. There are two anterior *lunulae*. The posterior aspect shows two posterior *lunulae*, a small mesial and a much larger lateral *lunula*‡. In *Varanus* the *cyamella* has become entirely anterior; it thus differs widely in position from the *cyamella* in higher mammalian forms. Cf. the Orang in our Plate XXVI, Figs. 68 and 69. This position of the *cyamella* is not universal in reptiles. Thus in *Trachysaurus rugosus*, the Australian stump-tailed lizard, the *cyamella* (see our Plate XXIV, Figs. 63 *a* and 63 *b*) is seen from *both* posterior and anterior aspects, and it is more easily confused with a *lunula* of the lateral semilunar. The knee-joint of this lizard has in addition two anterior *lunulae* and two posterior *lunulae*, of which the internal is larger than the external—exactly the opposite to what occurs in *Varanus*.

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* We have already indicated the difficulty of arguing as Gruber does the value of the knee-joint sesamoids to man in face of the fact that 90°/₀ of mankind do just as well without them.

† *Text-book of Zoology*, Vol. II. p. 524.

‡ In the specimen of *Varanus niloticus* mounted in the British Museum (Natural History) only the parafibula and the two anterior *lunulae* are visible.

Our third dissection was of a knee-joint of *Amphibolurus barbata*. Here we have no longer the parafibula, but posterior mesial and lateral *lunulae*, mesial anterior and lateral (or rather sagittal or trochlear) anterior *lunulae* (see our Plate XXIV, Figs. 65*a* and 65*b*). In this case the lateral posterior *lunula* is larger than the mesial, and there is a groove on the trochlear portion of the femur—exaggerated in the drawing to indicate its existence—which probably articulated with the sagittal *lunula*. In a very young specimen of *Iguana tuberculata* (*Lacertilia*) we were unable to find any parafibula; the posterior lateral *lunula* and the anterior sagittal *lunula* were present*. Mivart, who has studied the myology of *Iguana tuberculata*†, states that the outer head of *gastrocnemius* in this case arises from above the external condyle, that *plantaris* is very intimately connected with *gastrocnemius* and that *popliteus* arises from the *fibula*. He makes no mention of a parafibular sesamoid. In considering the absence of the parafibula this arrangement of the muscles should be borne in mind.

Specimens of *Agama stellio* and of a common lizard (*Lacerta vivipara*) dissected in our laboratory confirm the arrangement in *Varanus* of a parafibula with two anterior and two posterior *lunulae*.

In a specimen of *Spenodon punctata* examined no parafibula was found but only an anterior sagittal (mid-trochlear) *lunula*. This was confirmed from a mounted specimen of *Spenodon* seen at the South London Botanical Institute.

Mounted skeletons of the *Reptilia* do not as a rule afford much information, either when large on account of being over clean, or when small the knee-joints being often inaccessible even with the use of a lens to minute examination. They require dissection when moist. We may note the following observations made chiefly on specimens at the Royal College of Surgeons.

We examined three chameleons. In *Chamaeleo vulgaris*, we found a sesamoid at the top of the fibula and between this and external face of lateral condyle; there were no *lunulae* (or, of course, *fabellae*); the patella was ossified. In a specimen of *Chamaeleo verrucosus* there were cavities from which it looked as if parafibular sesamoids had fallen out. In a specimen of *Chamaeleo bifurcatus* nothing was distinguishable. In *Zonosaurus madagascarensis* there was an ossified patella, but no other visible knee-joint sesamoid. In *Eumeces algeriensis* there was a parafibula wedged between fibula and tibia; we also found a single *lunula*.

In *Corucia zebrata* there was a somewhat noteworthy system of knee-joint sesamoids. There was a sesamoid articulating with the head of the fibula and a second, directly connected by a ligament with the first, articulating with the head of the tibia; it would be easy to interpret either or both as cases of *lunulae*: see drawing, Plate XXXV, Fig. 91. There was a small ossified patella. Parafibular and paratibial sesamoids also occur in *Lacerta ocellata* together with an internal anterior *lunula*‡.

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* In a mounted specimen of *I. tuberculata*, we again found no parafibular sesamoid, but the anterior *lunula* was rather lateral than sagittal.

† *Proc. Zool. Society of London*, 1867, p. 795.

‡ This lizard had, but on the left limb only, what looked like a possible lateral *fabella*.

In *Tiliqua scincoides*, *Heloderma suspectum* (the Gila monster), *Amieva surinamensis* and *Callopestes* sp. we were only able to note the parafibular sesamoid.

In *Amblyrhynchus cristatus* only lateral posterior and anterior *lunulae* were visible.

In *Physignathus lesueuri* there were all four *lunulae*. In *Uromastix spinipes* there was a small lateral and large mesial posterior *lunulae* and possibly very small lateral and mesial anterior *lunulae*.

In *Jacare punctata* we found what was possibly a mesial posterior *lunula*, but this was doubtful. In no mounted specimens of crocodiles or alligators of a large size have we found parafibular sesamoid or *lunulae**.

(23) *Amphibia*.

Among the Batrachians we dissected two species of frogs without discovering any sesamoids at all in the knee-joint. We examined a large number of skeletons with the same result. There were, however, two possible exceptions. In *Leptodactylus pentadactylus* we believe that a mesial posterior *lunula* may exist, and in *Docidophryne gigantea* with more doubt a lateral posterior *lunula*.

Finally we may note that we have dissected specimens of *Trionyx gangetica* and *Testudo graeca* and found no ossifications at all in the knee-joint, even the patella being cartilaginous.

It will thus be seen that the *Amphibia* and *Reptilia* present a great variety of sesamoidal conditions in the knee-joint. We may start from no ossifications at all, even the patella being cartilaginous; we may have a single anterior sagittal *lunula*†, or again two anterior and two posterior *lunulae*; or we may find in *Lacertilia* all four *lunulae* associated with a parafibula.

We have no real evidence of any lateral *fabella* in this order. The origin of this must be sought in the break-up of the parafibula into *cyamella* and lateral *fabella* in a stage between marsupial and primitive placental. One point appears to us clear, that the appearance of *lunulae* in the higher orders is a vestige of a reptilian ancestry, even in the case where *lunulae* appear in the Primates (from Lemuroids to Man). Further the appearances of *cyamella* and lateral *fabella* are vestiges (even in Man) of an ancestry of primitive ornithodelphian character which had a parafibula, or possibly a fibular crest.

The origin of the mesial *fabella* seems to us shrouded in far greater mystery; it is always of secondary importance, often merely cartilaginous, still more often absent; it is not a "Knotenpunkt" of important muscle attachments like the lateral *fabella*. The cnemial crest of the tibia is relatively rare and has been very rarely indeed recorded in reptilian forms[*], and we do not know to what extent the inner head of *gastrocnemius* is associated with this crest[†]. The possibility of the cnemial crest having given rise to either or both patella and mesial *fabella* may indeed be borne in mind, but it is not of a high order of probability. One feels inclined to propound some general ontogenetic principle by which what occurs by evolutionary origin on one side of a member will be "sympathetically" (or cytologically?) shadowed on the other. Thus *lunulae*, *fabellae* or even condyles occur in pairs, and this is true also of muscular attachments and tuberosities. To propound such a principle would, however, be too venturesome[‡], and all we can assert is that the mesial *fabella* has certainly a different origin to the lateral. It is later in arriving and earlier in degenerating and never has the anatomical importance of its lateral colleague.

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* In a mounted specimen of *Crocodilus americanus* we noted what looked like a very tiny external *fabella*!

† The possibility of an anterior sagittal *lunula* being the source of a patella is possibly worth bearing in mind.

(24) *Conclusions.*

The main point that seems to us to arise from this study of the sesamoids of the knee-joint is that no parts of the mammalian skeletal form, however apparently insignificant, are without exceeding interest if time can be devoted to their study. If we take the whole evolution of the sesamoids of the knee-joint from their entire absence in the Amphibia to their culminating point in the *Tupaiidae* and *Sciuridae* and to their entire disappearance in certain *Pteropodidae*, we are compelled to admit the feebleness of the argument for use value in any case but that of the patella. Even in the case of the patella we have to admit that the Amphibia, many reptiles, the Marsupials, and some birds seem to have got on remarkably well

[*] The occurrence of reptilian forms with even moderate tibial crests should be of a very exciting character. The only case we have so far been able to discover is that of *Ceratosaurus nasicornis* Marsh, a carnivorous Dinosaur of the American Jurassic. It is figured by Marsh and the tibia has a large cnemial crest. It shows in certain respects other avian resemblances as in the form of the pubis and in the co-ossifications of all the pelvic and of the metatarsal bones: see "The Dinosaurs of North America," by O. C. Marsh, *Sixteenth Annual Report of the U. S. Geological Survey*, Part I. pp. 156—162, and Plate XIV, 1896.

[†] E. Coues in his paper on "The Osteology of *Colymbus torquatus*, with notes on its Myology" (*Memoirs of the Boston Society of Natural History*, Vol. I. 1863, pp. 131—172) deals with muscles of the knee-joint. In this case the tibial crest is as long as the femur itself (2″): see our Plate XXXVI, Fig. 94, and the author makes no mention of an independent patella. Indeed he writes (p. 159): "Just at the border of the joint there is a very small projecting process of bone, which is generally regarded as the true analogue of the patella." Of the muscles he states that *Cruraeus* has a very extensive muscular attachment to the posterior face of the whole length of the tibial spine which projects above the knee-joint (p. 168). *Semimembranosus* is inserted by a broad membranous tendon into the crest of the tibia (p. 170). *Gastrocnemius* might, it seems, almost be described as having four heads. Part of the inner arises fleshy from the apex of the tibial spine and from the anterior face of the upper two-thirds of the bone, the other portion of the inner arises from the inner condyle. The outer head arises from the *linea aspera* for nearly two-thirds of its length and from the outer condyle; it also receives attachments from the *rectus femoris* (p. 171). But the *rectus femoris* instead of going to the patella as in man is inserted in the head of the fibula (p. 167). It would thus appear that the inner head arises from inner condyle and tibial crest, the outer head from outer condyle but is linked also to head of the fibula. The femur articulates with tibia and fibula; the articulation of inner condyle is tibial; that of outer condyle partly tibial, but most extensively fibular (p. 159). Without being conclusive this description is most suggestive for the possibility of the origin of the patella from the tibial crest and to a lesser extent of the origin of a mesial fabella from the same source.

[‡] The tendency, however, to reach greater complexity by doubling may, perhaps, be traced in various organs, e.g. in the olfactory organ, or the evolutionary history of the ventricle of the heart.

without ossified patellae. If it be argued that this depends on a difference of mode of progression, a similar counter can hardly be made to the arguments adopted in favour of a use value for the *fabella*; these arguments are too strong, the *Anthropoidea* ought never to have lost their *fabellae*! If we take what appears to us the more rational view that all the sesamoids of the knee-joint are vestigial, and are debris of one or more structures originally of use value, we are bound to consider some such scheme as that of the accompanying diagram, and then the chief difficulty of linkage is seen to be at once apparent in the question as to how far the sesamoids in the knee-joint of any existing species are to be accounted for by acquisition or lapse. For example, the bear and the sheep possess the patella alone: are we to assume their ancestors have never possessed or have lost a complete system of knee-joint sesamoids? The frog and some species of bat possess no sesamoids at all of the knee-joint, but the former has never acquired them, and in the latter they have been suppressed in a long course of evolution. So it is with sheep and bear; the former belongs to the Ungulates who give no evidence of ever having developed a knee-joint sesamoid* beyond the patella, and the latter to the Carnivores with an elaborate evolutionary history of knee-joint sesamoids as complex as that of the Rodents or Insectivores. Again those who like Abel assume the Pinnipedia to have sprung from the *Ursidae*† seem to overlook the relationship of the latter to the full knee-joint sesamoid system of the Carnivores—especially to the *Canidae*.

Or, to go a stage further, we have so far not come across any Insectivores with patella only. Edentates of this character exist, but the Insectivore with only a patella has yet to be found. It may have existed, but the Insectivores seem to have sprung from a multi-sesamoidal form. Chiroptera and Rodentia can well have sprung from the Insectivores. To suggest as Kükenthal‡ that the Ungulates sprung from the Insectivores and the latter from Marsupials, is to neglect the fundamental contribution of the Marsupials to the knee-joint sesamoid system, namely, the *cyamella* and the lateral *fabella*. The parafibula is known in reptilian forms and the Edentates may have got their parafibula from these. But if the Ungulates sprung from the Marsupials it is astonishing that no cases even as anomalies of the *cyamella* in the Ungulates have been recorded.

We may note also a very special point of difficulty about the Marsupials themselves. An ossified patella is an extreme rarity. Are we to assume that the patella was lost in the Marsupials while *cyamella* and *fabellae* were developing? The ossified patella exists in the Monotremes, and this alone would differentiate them largely from the Marsupials. But if the patella was obtained in the reptilian stage and handed on to the Monotremes and certain birds, while it was lost in the Marsupials, it is hard to believe in a direct descent of Insectivores from Marsupials, at any rate it would point either to the *Peramelidae* or to some other Marsupial differing widely—as far as the knee-joint is concerned—from those hitherto known.

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* The lateral *fabella* of *Hyrax* we take to be evidence, not of a lost sesamoidal system in the Ungulates, but of a differentiated origin of *Hyrax*. We have not been able to confirm Meckel's and Gruber's statements as to the *Cervidae*.

† *Handwörterbuch der Naturwissenschaften*, Bd. VIII. S. 718, 1913.

‡ *Ibid.* Bd. VIII.

A study of either Carnivores or Primates indicates what a long course of evolution is involved in the loss of a sesamoidal system, and what a wide range of changing forms usually intervenes. The persistency of the same type of sesamoidal system for generations in the same species, and the occurrence of atavisms, such as *lunulae* in man, form strong evidence that the minor sesamoids of the knee-joint are as hereditary in character as the patella.

To assert that a sesamoid can be produced by "intensive stress" when and where it is required is to assert in its baldest and most futile form the inheritance of acquired characters. The most futile form because a parafibula, say, is not a merely formless mass; it is an organised link for a system of muscles, usually of a very elaborate kind. And if it could be acquired by "intensive stress" when and where needed, there would seem no reason to despair of any species producing a new bone of the skeleton, when and where needed. It is conceivable that a mutation could produce such a bone by an anomalous disturbance of the germ cells—but it would certainly not be due to "intensive stress" at the required point, and it would only be by the rarest chance that it would be "when and where needed." The whole mechanism of heredity is disregarded by such anatomical suggestions.

In forming the scheme of our diagram we wish to emphasise the fact that while there are factors of acquisition and suppression at work, we yet consider the primary factor to be heredity—the form of the sesamoidal system is inherited as the form of the teeth are inherited, and the change of form will in each case be a lengthy evolutionary process*.

In our diagram we have purposely refrained from providing any descent links, partly because there is such an immense amount of work still to be done on the sesamoid systems especially of reptilian and avian forms, and partly because to do so would be sure to give rise to the criticism that we had supposed one illustrative type to have sprung directly from a second illustrative type; whereas in fact both illustrative types may have been only *in cunabula* at the time of the link. The link lies between the sesamoidal systems, not necessarily between their present representatives.

We have really four origins to study:

(*a*) That of the patella; it may have arisen from the tibial crest or from an antero-sagittal *lunula*, or perhaps have had both origins. At present we have not come across any evidence of a tibial crest in the Reptilia except in the Dinosaurs.

(*b*) That (or better, perhaps, those) of the *lunulae*. We have no suggestion to make here. It needs a far greater study of the knee-joint of both Amphibia and Reptilia than we have been able to make.

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* That in an early period of evolution the germ cells of various allied species were not so highly specialised and differentiated as in a later period, is a possibility that we have not seen emphasised, and which would, perhaps, render by hybridisation the earlier evolutionary processes quicker. Even now we have very vague ideas of the limits of possible hybridisation. How far are the Primates *inter se* fertile? The fox and dog are natural enemies, but the cross is a feasible one, and will provide a second generation. Much of importance for evolution might arise by crossing—if needful by artificial impregnation—forms apparently fairly diverse. Divergence of habits and temperament and somatic differences may have more to do with the problem of infertility than any factor of the germ cells themselves.

To face p. 90

THE EVOLUTION OF THE ORTHOSESAMOIDS OF THE KNEE-JOINT (INCLUDING THE PATELLA).

←—*Acquisition*

No Sesamoids
(Most *Amphibia*)

No Sesamoids
(Some *Reptilia*)

Single Lunula
(Some *Amphibia*? e.g. *Leptodactylus pentadactylus*)

No Sesamoids

Lunulae
(Some *Reptilia*, e.g. *Amphibolurus barbata*)

Tibial Crest
(Some *Reptilia* ?)

Fibular Crest
(Some *Reptilia* ??)

Tibial Crest

Tibial Crest and Lunulae
(Some *Aves*)

Tibial Crest and Lunulae
(Some *Reptilia* ?)

Parafibula and Lunulae
(Some *Reptilia*, e.g. *Varanus*)

Patella and Fibular Crest
(Monotremes)

Tibial Crest
(Some *Aves*, e.g. Albatross)

Tibial Crest, Flake Patella and Lunulae
(Some *Aves*, e.g. *Colymbus*)

Patella, Parafibula and Lunulae
(Some *Reptilia* ? e.g. *Corucia zebrata*)

Parafibula
?

Fibular Crest
(Some Marsupials, e.g. occasionally Wombat)

Patella and Lunulae
(Some *Aves*)

Patella, Parafibula and Lunulae
?

Parafibula
(Some Marsupials; usually Wombat)

Patella
(Some Edentates, *Dasypus*, *Chlamydophorus*)

Patella and Lunulae
?

Patella, Parafibula and Lunulae
(Some Edentates, *Megatherium*, *Bradypodidae*, *Manidae*)

L. Fabella and Cyamella
(Some Marsupials, e.g. *Macropus*)

Patella
(Some Insectivores??)

Patella and Lunulae
(Some Insectivores, Myogale, perhaps)

Patella, Lunulae, L. Fabella
(Some Insectivores, e.g. *Talpa*, *Potamogale*)

Patella, and L. Fabella
(Some Edentates? *Orycteropus*)

Patella and Cyamella
(Some Edentates, e.g. *Myrmecophaga*)

Patella, Cyamella and (or fused with) L. Fabella
(Some Marsupials, e.g. *Perameles*, bony kernel to patella in others)

Patella
(*Ungulata*, *Pinnipedia*)

Patella and L. Fabella
(*Hyracoidea*. ? Some *Cervidae*)

Patella, Lunulae, L. and M. Fabella
(Some Insectivores, e.g. *Erinaceus*, *Tupaia*, *Hylomys*)

Patella, Cyamella, Lunulae
(Some Insectivores, e.g. *Ericulus setosus*)

Cyamella and (or fused with) L. Fabella, M. Fabella
(asserted of *Halmaturus*)

←—*Lapse*

Patella and Lunulae
(Some Rodents, e.g. *Castor fiber*)

Patella, Lunulae, L. and M. Fabellae
(Some Rodents, e.g. *Mus musculus*, *Fiber zibethicus*, *Dasyprocta*)

Patella, Lunulae, Cyamella, L. and M. Fabellae
(Some Lemuroids, e.g. Loris and Potto)

Patellae, Lunulae, Cyamella, L. and M. Fabellae
(Some Rodents, e.g. Rabbit, Squirrel)

Patella, Cyamella, L. and M. Fabellae
(Probable ancestor of *Chiroptera*)

Patella, L. and M. Fabellae, Cyamella
(Some Carnivores, e.g. *Felis domestica*)

Patella, Cyamella, L. and M. Fabellae
(Some Lemuroids, e.g. *Chiromys*; *Cebidae*, and *Simiadae*)

Patella, L. and M. Fabellae
(Some *Chiroptera*, e.g. *Cynopterus marginatus*)

Patella, L. and M. Fabellae
(Some Carnivores, e.g. *Felis nebulosa*)

Patella and Cyamella
(Some *Anthropoidea*, Orang, Gorilla)

Patella, L. and M. Fabellae
(Certain *Hylobatinae*)

Cyamella, L. and M. Fabellae
(Some *Chiroptera*, e.g. certain species *Vespertilio*)

Patella and L. Fabella
(Some Carnivores, e.g. *Lutra*, *Gula vittatus*)

Patella
(Some *Anthropoidea*, Chimpanzee, and *Hominidae*, Man)

Patella and L. Fabellae
(Certain *Hylobatinae*

L. and M. Fabellae
(Some *Chiroptera*, e.g. *Vespertilio murinus*)

Patella
(Some Carnivores, e.g. *Ursus*)

L. Fabella
(Some *Chiroptera*, e.g. *Phyllostoma*)

No Sesamoids
Some *Chiroptera*, e.g. certain species *Pteropus*)

(*c*) That of *cyamella* and lateral *fabella*. We are fairly convinced that this lies in the break-up of the parafibula and that the parafibula was the result of the separation of the fibular crest with its attached muscular system. The parafibula exists in certain reptiles. The discovery of a reptilian fibular crest would be of the greatest importance. Of course there may be again a double origin corresponding to the parafibula of the Reptiles and the fibular crest of the Monotremes.

(*d*) That of the appearance at a relatively late stage of evolution (and the early disappearance) of the mesial *fabella*. We have no real light to throw on this point; it needs a very special study. The fact that the mesial *fabella* is never specific without the lateral, while the lateral is in early as well as in late evolutionary stages specific without the mesial, suggests that the explanation may be cytological. At the same time we have to remember that while the lateral head of *gastrocnemius* had originally a fibular or at least a parafibular attachment, the evolutionary history of the inner head seems to point to no such marked change in its attachments*.

The object of this memoir has been to suggest problems to those better equipped for studying them than the present authors, rather than to present solutions. They believe that the least important elements of the skeletal form are each able to contribute important suggestions for the general attack on the enigma of evolution and that all vestiges are of special value in the assault. They might even be content with the outcome of this paper if it led anatomical text-book writers in the future to drop once for all the Galen tradition and assert on the contrary that it is needful that all sesamoids should be discussed.

As final conclusion may we not cite the words used by Pittard in 1849 as appropriate to our own views: "But after all, taking into consideration all the facts related above, and many others that have presented themselves to us in the course of this enquiry, we cannot but believe that some higher law than that of adaptation concurs in determining the presence, if not the size, of even these little bones†."

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* It may have in certain cases an insertion to the tibial crest: see the second footnote on p. 88.

† Article on Sesamoid Bones, Todd's *Cyclopaedia of Anatomy and Physiology*, p. 543.

DESCRIPTION OF PLATES XIX—XXXVII*.

Plate XIX, Fig. 40. Femur of Sea Otter (*Enhydra lutris*), showing the marked development of the lateral *fabella*; the sesamoid appears by its action to have largely eroded the popliteal surface of the femur, and the periosteum of the bone in its neighbourhood has disappeared.

Fig. 41. Fibula, Tibia and Femur of Beaver (*Castor fiber*). The development of the fibular head at A suggests how a second sesamoid might well originate in the tendon of the muscle (*Peroneus longus*?) attached to this projection. The femur exhibits a marked third trochanter.

Plate XX, Fig. 42. Drawing of musculature of knee-joint of *Ornithorhynchus*. We see the lateral head of *M. gastrocnemius* attached solely to the fibular crest; the mesial head of *gastrocnemius* is still attached to the mesial condyle.

Fig. 43 *a*, anterior, and Fig. 43 *b*, lateral aspect of the femur, tibia and fibula of *Ornithorhynchus*. The fibula shows the noteworthy crest, a compressed process with its own centre of ossification. There are no sesamoids except patella. Cf. Fig. 47 for the corresponding bones of *Echidna*.

Fig. 44. Drawing of the posterior aspect of the left knee-joint of *Felis domestica*, showing the positions of the external (*e.f.*) and internal (*i.f.*) *fabellae*, the *cyamella* (*cy.*) and the facet on which the latter rests. Owing to the knee-joint being slightly extended the *cyamella* has been lifted off its articular surface on the head of the fibula†.

Fig. 45. Drawing of postero-lateral aspect of the left knee-joint of *Hyrax* showing the external *fabella* (*e.f.*) above the external condyle, but the tendon of *gastrocnemius* has shrunk in drying, so that the *fabella* has been lifted off the condyle. There is a slight depression on the internal condyle, which might suggest an internal *fabella*, but so far none has been found.

Plate XXI, Fig. 46. *Colymbus glacialis*, a drawing after Owen's figure in his article *Aves* in Todd's *Cyclopaedia*. Note the remarkable cnemial crest of the tibia. Cf. especially all the figures on Plate XXXVI.

Fig. 47. Lateral aspect of pelvic limb of *Echidna* to be compared with the knee-joint of *Ornithorhynchus* in Figs. 43 *a* and 43 *b*. Drawing after a part of the skeleton in a plate of Cuvier's *Recherches sur les ossemens fossiles*, Paris, 1834–6 (Tome II, Atlas Plate 214).

Fig. 48. Drawing of lateral, Fig. 49, drawing of mesial, aspect of knee-joint of left limb of Cereopsis Goose, showing cnemial crest of tibia and also a semi-fibular crest which works in a groove on the articular surface of the lateral condyle. Cf. Plate XXXVI.

Plate XXII, Figs. 50 and 51. Drawings from lateral and mesial aspects of the left knee-joint of the Albatross, showing the remarkable cnemial crest of the tibia.

Figs. 52, 53 and 54. Drawings of anterior, lateral and posterior aspects of knee-joint of *Dendrocygna*, the Tree Duck. There is a cnemial crest (*cn. crest*), internal (*i.p.lu.*) and external (*e.p.lu.*) posterior *lunulae* and also what appear to be two or three very small sesamoids wedged in between fibula and tibia (*sesamoids*). Cf. Plate XXXVI.

Plate XXIII, Fig. 55 *a*. Tamandua Anteater (*Tamandua tetradactyla*); photograph of posterior aspect of right limb showing the large *cyamella* (*c.*) still in the popliteal tendon.

Fig. 55 *b*. Common Squirrel (*Sciurus vulgaris*), photograph of posterior aspect of right limb, showing internal and external *lunulae* (*i.l.* and *e.l.*) and *cyamella* (*c.*). Both *fabellae* also exist in the squirrel.

Figs. 56 *a* and 56 *b*. Common Hedgehog (*Erinaceus europaeus*). The former photograph of posterior aspect of right limb showing internal (*i.f.*) and external (*e.f.*) *fabellae*; the latter photograph of mesial aspect of left limb with the femur doubled right back to show anterior external (*a.e.l.*) and anterior internal (*a.i.l.*) *lunulae*. No *cyamella* was found.

Fig. 57 *a*. Photograph of the right pelvic limb of *Hydromys chrysogaster*, the Golden-bellied Rat, from the posterior aspect showing internal (*i.f.*) and external (*e.f.*) *fabellae*.

* The drawings are as a rule natural size.

† It must be remembered that in nearly all these drawings the sesamoid bones are still contained in the tendons in which they occur. Consequently no attempt could be made to show the actual size of the sesamoids.

Fig. 57 *b*. Photograph of the posterior aspect of the right pelvic limb of *Fiber zibethicus*, the Musquash, showing internal (*i.f.*) and external (*e.f.*) *fabellae* together with a posterior external *lunula* (*p.e.l.*). Compare Figs. 61 *a* and 61 *b*.

Plate XXIV, Fig. 58. Drawing of posterior aspect of left pelvic limb of *Lepus cuniculus*, the Common Rabbit, showing large external (*e.f.*) and smaller internal (*i.f.*) *fabellae* and *cyamella* (*cy.*). The rabbit has usually (?) two anterior *lunulae* as well, but not in this specimen.

Fig. 59. Drawing of lateral aspect of left pelvic limb of *Potamogale velox* from West Africa, showing the external *fabella* (*e.f.*). No sign of ossification in popliteal tendon. Fibula fused with tibia at distal end.

Fig. 60 *a*. Drawing of posterior aspect of left knee-joint of *Paraxerus jacksoni*, African Squirrel, showing external (*e.f.*) and internal (*i.f.*) *fabellae*, together with *cyamella* (*cy.*).

Fig. 60 *b* is the anterior view of the same knee-joint showing an internal anterior *lunula* (*a.i.lu.*).

Fig. 61 *a* and Fig. 61 *b*. Drawings respectively of the posterior and anterior aspects of the right knee-joint of *Fiber zibethicus*, the Musquash or Musk Rat. The former shows the internal (*i.f.*) and external (*e.f.*) *fabellae* with a posterior external *lunula*; the latter besides the two *fabellae* shows external (*e.a.lu.*) and internal (*i.a.lu.*) anterior *lunulae*, but no *cyamella* was present. Cf. Plate XXIII, Fig. 57 *b*.

Fig. 62 *a* and Fig. 62 *b* provide drawings of the posterior and postero-lateral aspects of right pelvic limb of *Hylomys suillus dorsalis*, a Tree Shrew from Borneo. Only internal (*i.f.*) and external (*e.f.*) *fabellae* were found.

Fig. 63 *a* and Fig. 63 *b*. Drawings of the anterior and posterior aspects of the knee-joint of *Trachysaurus rugosus*, the Australian stump-tailed lizard. The former shows at *a′* the lateral anterior *lunula*, and at *b′* the mesial anterior *lunula*; the latter gives *a* the mesial and *b* the lateral posterior *lunula*, and the *cyamella* as indicated. The *cyamella* is on the *anterior* corner of the fibula, but is seen in both posterior and anterior aspects. The four *lunulae* all lie between tibia and femur, the *cyamella* between fibula and femur.

Fig. 64 *a* and Fig. 64 *b*. Drawings of the posterior and anterior aspects of the right knee-joint of *Varanus niloticus*, the Nile Monitor. The former shows internal (*p.i.lu.*) and external (*p.e.lu.*) posterior *lunulae* and the latter external (*a.e.lu.*) and internal (*a.i.lu.*) anterior *lunulae* as well as a large *cyamella* or better *parafibula* (*paraf.*) on the head of the fibula. This parafibula has tendon in the popliteal groove and is also attached to the head of the fibula; it lies just internal to the attachment of the external lateral ligament as shown in the drawing (Fig. 64 *b*). It will be seen that the *cyamella* is entirely anterior and this position is in partial agreement with that of *Trachysaurus rugosus*, which, however, is also visible from posterior as well as anterior aspect. Cf. Figs. 63 *a* and 63 *b*.

Fig. 65 *a* and Fig. 65 *b*. Drawings of the anterior and posterior aspects of the left knee-joint of *Amphibolurus barbata*. The former shows two anterior *lunulae*, a small internal one (*a.i.lu.*) and a larger external (*a.e.lu.*) or rather mid-trochlear *lunula*. The latter shows an external (*p.e.lu.*) and an internal (*p.i.lu.*) posterior *lunula*; both are on top of the tibia and the external is the larger. There is no trace of a parafibula.

Plate XXV, Fig. 66. Photograph of the right knee-joint of *Megatherium cuvieri* or the Fossil Giant Sloth, in the Royal College of Surgeons' Museum. The photograph shows a sesamoid on the top of the fibula, which has usually been described as a lateral *fabella*. It lies close to the popliteal groove and there is little doubt that it is a *cyamella* (*cy.*) or rather parafibula. On the top of the tibia is a second sesamoid which we have not hitherto seen referred to. It is undoubtedly an external anterior *lunula* (*a.e.lu.*). It lies externally from the base of the large *patella* (*pa.*).

Fig. 67. Photograph of the left knee-joint of *Manis aurita*, the Chinese Pangolin. The knee-joint has been opened out for the purpose of photography, but the *cyamella* (*cy.*), usually described as a *fabella*, appears to have been mounted in the right position. When the knee is flexed the sesamoid does not lie on the top of the external condyle, but on the top of the fibula; it is a parafibula, articulating with both fibula and the *posterior* face of the external condyle.

Plate XXVI, Fig. 68. Drawing of the posterior aspect of left knee-joint of *Simia satyrus*, the Orang-ûtan, showing the *cyamella* (*cy.*) in position in the popliteal tendon. Inset, drawings of three *cyamellae* from three Orang-ûtans' knee-joints dissected in the Biometric Laboratory, posterior and anterior aspects.

showing range of sizes from *b* to *c* and *a*. *a* is from Orang-ûtan figured, *b* and *c* are from a second specimen, left and right joints respectively. No other sesamoids were found.

Fig. 69 is a drawing of the same knee-joint as in Fig. 68 with the popliteal tendon containing the *cyamella lateralis* (*cy.*) turned back so as to disclose the facet (*f. for cy.*) on which it articulates.

Plate XXVII, Fig. 70 *a* and Fig. 70 *b*. Drawings from posterior and lateral aspects respectively of the left knee-joint of *Lemur varia*, showing the external (*e.f.*) and internal (*i.f.*) *fabellae*, the *cyamella* (*cy.*) and an anterior external *lunula* (*a.e.lu.*) in position. The *cyamella* is seen in close relation to the head of the *fibula* and one notes how with flexed limb the external *fabella* will come into contact with it.

Fig. 71 *a*. Drawing of posterior aspect of right knee-joint of *Mycetis palliatus*, showing internal *fabella* (*i.f.*), external *fabella* (*e.f.*) and *cyamella* (*cy.*).

Fig. 71 *b*. Sesamoids from the joint in Fig. 71 *a*. *a* is posterior aspect, *b* anterior aspect of *cyamella*, *c* and *d* are respectively *fabella mesialis*, and *fabella lateralis* in posterior aspects.

Fig. 72. Drawing of distal extremity of right femur of a Gibbon (*Hylobates lar*) which possessed only an internal sesamoid (*i.f.*) and no ossification in the popliteal tendon (*p.t.*) which was "horny" but not ossified.

Fig. 73. Drawing of postero-lateral aspect of left knee-joint of *Lemur melanocephalus* showing external (*e.f.*) and internal (*i.f.*) *fabellae*, the *cyamella* (*cy.*) enclosed in popliteal tendon, and an anterior external *lunula*.

Plate XXVIII, Fig. 74 *a*. Drawing of posterior aspect of left knee-joint of *Chiromys*, the Aye-Aye. The two branches of *M. gastrocnemius* (g_1 and g_2) have been deflected to show the external (*e.f.*) and the internal (*i.f.*) *fabellae* lying beneath; below is the popliteal tendon (*p.t.*) with the *cyamella* lying on the head of the fibula (*fib.h.*) and articulating with the tibia. *po.* is the popliteal muscle.

Fig. 74 *b*. Drawing of the lateral aspect of the left knee-joint of *Chiromys* after Owen (*Trans. Zool. Soc. London*, Vol. v, 1866, Plate XIX) to indicate how in flexure of the knee the external *fabella* (*e.f.*) comes in contact with the *cyamella* (*cy.*).

Fig. 75. Drawing in posterior aspect of left knee-joint of *Lemur catta*, showing external (*e.f.*) and internal (*i.f.*) *fabellae*, the *cyamella* (*cy.*) and an anterior external *lunula* (*a.e.lu.*).

Fig. 76. Drawing of the lateral aspect of the left knee-joint of a dry specimen of *Perodicticus potto*, Bosman's Potto, showing the position of the anterior external *lunula* (*a.e.lu.*) and the *cyamella* (*cy.*) on the head of the fibula. The popliteal tendon sends a branch down to the head of the fibula (see our p. 74). The *fabellae* had disappeared from this specimen, but it is clear that, in this flexed position of the limb, the lateral *fabella* must rest on the proximal surface of the *cyamella*.

Fig. 77. Drawing of the lateral aspect of the left knee-joint of *Indris brevicaudata*, the Indri, showing the popliteal tendon (*p.t.*) containing the *cyamella* (*cy.*) and the positions of external (*e.f.*) and internal (*i.f.*) *fabellae*. The intimate relations of external *fabella* and *cyamella* on complete flexure are again indicated.

Plate XXIX, Fig. 78. Right, photograph of right pelvic limb of *Phascolomys wombatus*, the Wombat. This specimen shows the parafibula absolutely fused to the fibula so as to show one continuous bone with very small indication of position of union.

Left, photograph of right pelvic limb of *Sarcophilus ursinus*, the Tasmanian Devil; the parafibula is united to the fibula, but its limits are more clearly defined.

Fig. 79. Photograph of left pelvic limb of Wombat, the two portions of the parafibula, which is really free of the fibula, are shown in position on the head of the fibula, the femur is tied back to show up the parafibula which in the usual flexed position would be in contact or almost in contact with the shaft of the femur.

Plate XXX, Fig. 80. Photograph of the left pelvic limb of *Phalangista vulpina*, the Wolfine Phalanger, showing the free parafibula (*paraf.*) mounted on the head of the fibula and its relation to the femur when the limb is flexed. The two portions of the parafibula, which ultimately become the lateral *fabella* and the *cyamella*, are easily distinguished.

Plate XXXI, Fig. 81. Drawing of the posterior aspect of the right knee-joint of the Wombat with muscles attached. Description chiefly on figure itself. The external *gastrocnemius* has been cut across and the proximal portion deflected to show parafibular sesamoid lying in its fibres, and the surface of the fibula with which the sesamoid articulates. The internal *gastrocnemius* takes origin from nearly the whole of the popliteal surface, while the external *gastrocnemius* originates from the parafibular sesamoid. The drawing is also intended to show the tendinous fibres running from *gastrocnemius externus* to the lateral border of the patella; a few, cut through in drawing in order to expose the patella, run to the lateral face of the external condyle. The popliteal tendon can also be seen taking origin in the popliteal groove of the external condyle. It passes across the head of the fibula, its internal border being connected with the external semilunar cartilage, while the external fibres run down to the muscle fibres of the popliteus. This latter arises from the upper third of the posterior surface of the fibula. The double nature of *gastrocnemius externus* suggests that the deeper portion is *soleus*, although Macalister ("Myology of the Wombat and the Tasmanian Devil," *Annals of Natural History*, 1870, p. 19 (offprint)) suggests that *soleus* has a fibular origin.

Plate XXXII, Fig. 82*a* and Fig. 82*b*. Drawings of the posterior aspect of the left pelvic limb of *Phascolarctus cinereus*, the Koala, with the muscles attached. Fig. 82*a* shows the popliteal muscle and the external *gastrocnemius* with the parafibular sesamoid covered by its fibres. Fig. 82*b* shows *gastrocnemius* cut and turned back, so that the facet of the sesamoid which articulates with the fibula is exhibited and the position on which it rests on the fibular head is seen. This sketch is also intended to illustrate the following relations. The fleshy portion of *popliteus* is attached to fibula, and popliteal tendon runs from the anterior proximal corner of fibula to popliteal groove on external condyle. Also tendinous fibres from the fleshy portion on fibula cross the posterior surface of the latter and mingle with the tendinous fibres of *gastrocnemius* which run from the sesamoid to the external condyle. (See also Fig. 86.)

Plate XXXIII, Fig. 83*a* and Fig. 83*b*. *Macropus* sp. The portion of the knee-joint of a kangaroo (species?) here drawn was most kindly sent to us by Dr W. C. Mackenzie of the Australian Institute of Anatomical Research. It consists only of the lateral branch of *gastrocnemius* with its sesamoid and the *cyamella*, together with the external semilunar cartilage attached. It was thus not possible to draw these in their natural position. It should not be impossible, however, to understand the relations to other structures if the reader will compare these drawings with those of other *Marsupialia*. The three important components are the external *fabella*, the cartilaginous *cyamella*, with surface which articulates with the fibular head, and the external semilunar cartilage. These are drawn in two aspects, the interesting point being that in the kangaroo the lower part of the parafibula, still articulating with the fibular head on the distal face and with the external *fabella* on the proximal has become purely cartilaginous.

Fig. 84. Drawing of the posterior aspect of the left knee-joint of *Didelphys virginiana*, the Virginian Opossum. Here *a* is the popliteal tendon from groove on external condyle, *b* is the *cyamella* in the popliteal tendon as it passes over fibular head, *c* and *d* are branches of popliteal muscle running from tendon attached to *cyamella*, *e* is the external *fabella* in tendon of *gastrocnemius*, *g* and *g′* are the cut ends of *gastrocnemius*. The *gastrocnemius* has been cut just below its insertion on top of the external condyle to enable it to be pulled aside and display the *fabella*. When the leg is fully flexed the external *fabella* lies on the external condyle, and the *cyamella* is in direct contact with the lower surface of the condyle and the *fabella*.

Fig. 85. Drawing of the lateral aspect of the left knee-joint of *Phalangista vulpina*, the Wolfine Phalanger. *a* is the parafibular sesamoid resting on the head of the fibula, *b* is the popliteal tendon. If the reader will compare this drawing with Fig. 78, he will grasp how parafibula and fibula united give a single complete bone. It is not possible to term the sesamoid of Phalangista merely a *fabella*.

Fig. 86. A further drawing of the posterior aspect of the right knee-joint of *Phascolarctus cinereus* after removal of the muscles. *a* is the tendon of *gastrocnemius externus* attached to femur above external condyle, *b* is the cut end of *gastrocnemius externus*, *c* is the fibular "collateral" ligament, *d* is the popliteal tendon running to head of fibula, the lower portion of popliteal tendon has been removed. From a specimen kindly sent by Dr W. Colin Mackenzie.

Plate XXXIV, Fig. 87. Femur of *Macropus bennettii*, the Wallaby, with parafibular sesamoid attached above the external condyle.

Fig. 88. *Perameles lagotis*, the Rabbit-eared Perameles, with parafibular sesamoid attached above the external condyle.

Figs. 87 and 88 are photographs of museum specimens and we hold that they place the sesamoid in an erroneous position, leading it to be confused with a lateral *fabella*.

Fig. 89 *a* and Fig. 89 *b*. Photographs of anterior and lateral aspects of a moist preparation of the right knee-joint of *Sarcophilus ursinus*, the Tasmanian Devil, from the Museum of the Royal College of Surgeons, showing the parafibular sesamoid in what we believe to be the true position, i.e. mounted on the head of the fibula with a ligament connecting its summit with the lateral face of the femur above the external condyle.

Plate XXXV, Fig. 90. Drawing of the lateral aspect of the right knee-joint of *Halmaturus sp.*, the Wallaby, to indicate the position of the parafibular sesamoid on the head of the fibula.

Fig. 91. Drawing of the postero-lateral aspect of the left limb of *Corucia zebrata* to show a noteworthy sesamoid arrangement. *a* is a parafibular sesamoid united by a ligament to *b* a paratibial sesamoid, which might be a *lunula*. Drawing by Mr S. Steward.

Plate XXXVI. Drawings of the knee-joints of Birds. Cf. Plate XXI, Figs. 46, 48, 49, and Plate XXII, Figs. 50, 51, 52, and 53.

Fig. 92. Drawing of lateral aspect of left pelvic limb A of *Hesperornis regalis*, after Marsh. Note the giant patella—longer than femur—and the condyles of the femur enclosed by patella; tibia and fibula.

Fig. 93 *a* and Fig. 93 *b* give the mesial (B_1) and lateral (B_2) aspects of the right and left knee-joints of the Cormorant; the patella is of relatively smaller size than that of *Hesperornis regalis*, but clearly built on the same lines; the continuity of the ridges *aa′* and *bb′*,—the pro- and ecto-cnemial ridges of the tibia carried right up the lateral face of the patella,—must be emphasised, as in favour of released cnemial crest rather than a co-ossified patella.

Fig. 94. Drawing of the lateral aspect of the left pelvic limb C of *Colymbus torquatus* after Coues. There is a giant cnemial crest. A comparison of A and C suggests either that (i) the cnemial crest is a co-ossified patella or (ii) the patella a released cnemial crest; independent origin of both is hard to accept. B_2 is certainly an argument in favour of (ii).

Plate XXXVII, Fig. 95 and Fig. 96. Drawings of sections respectively of the fibular crest of a young and an embryo platypus. In the former case ossification is complete but the arrangement of the Haversian canals at the top of the plate, i.e. the proximal end of the fibular crest, seems far from incompatible with a separate centre of ossification. In the latter there appear signs of ossification starting towards the summit of the crest in an area widely removed from the centres of ossification of the shaft or of the fibular head.

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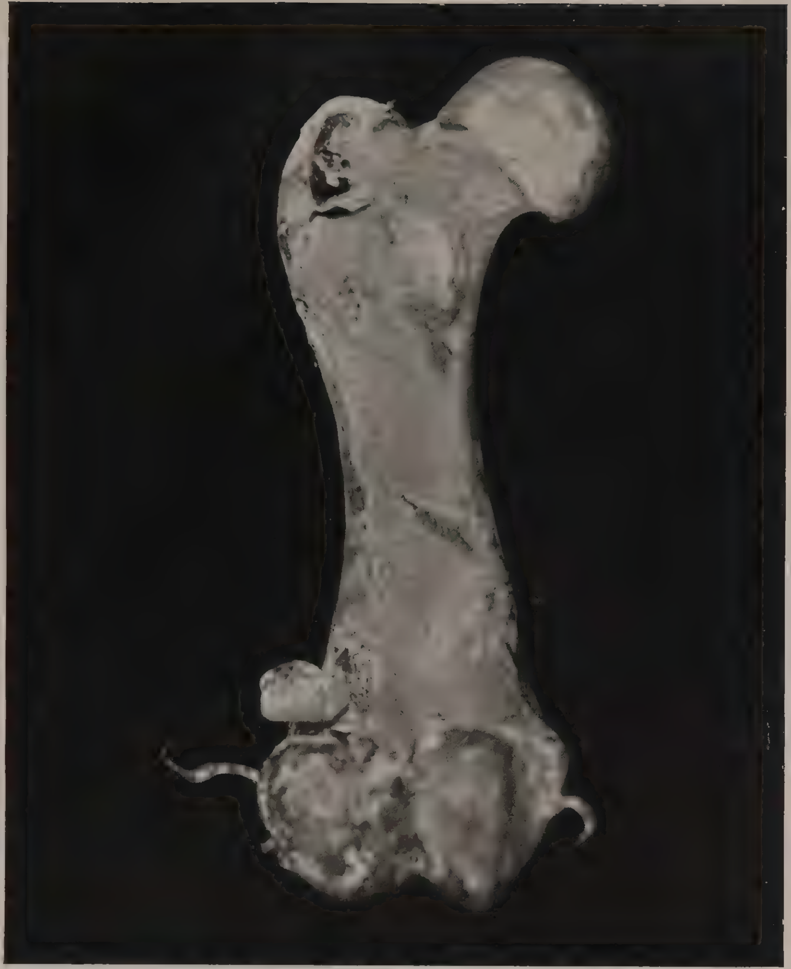


Fig. 40. Femur of Sea Otter (*Enhydra lutris*).

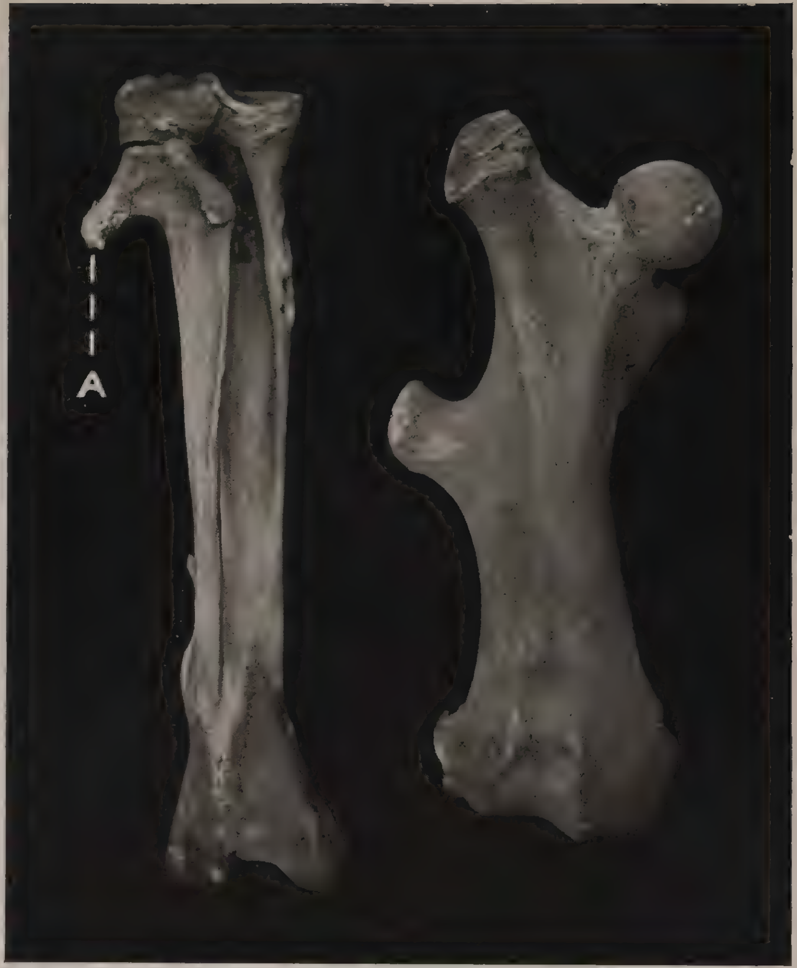


Fig. 41. Fibula, Tibia and Femur of Beaver (*Castor fiber*).

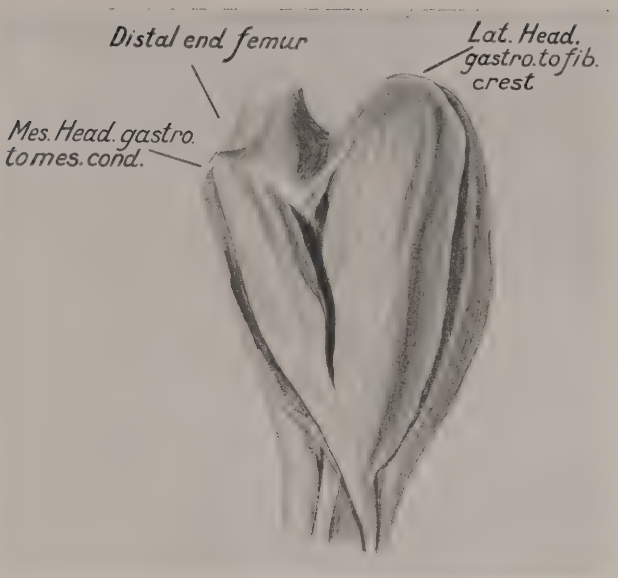

Distal end femur
Lat. Head. gastro. to fib. crest
Mes. Head. gastro. to mes. cond.

Fig. 42. *Ornithorhynchus* (Musculature).

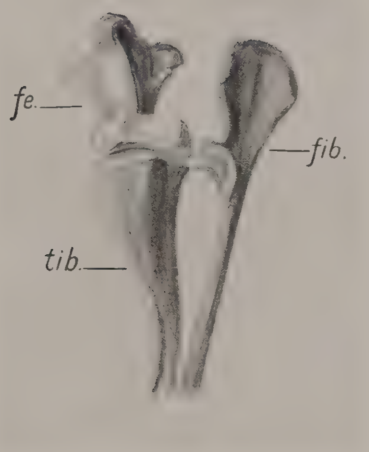


Fig. 43 *a*.

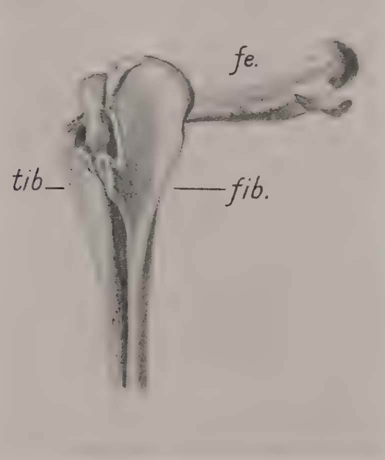


Fig. 43 *b*.

Ornithorhynchus (Bones of Lower Limb).

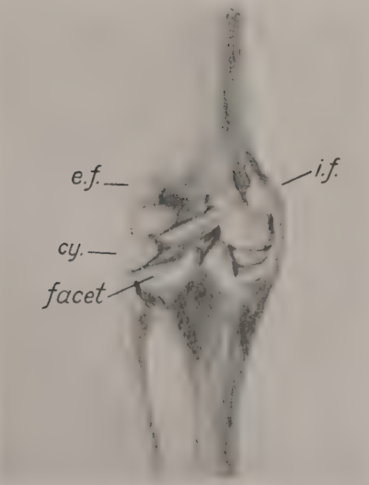


Fig. 44. Cat (*Felis domestica*).

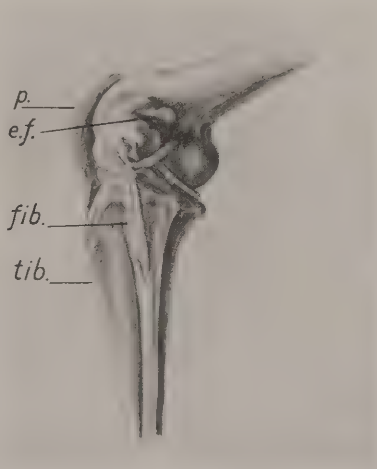


Fig. 45. *Hyrax*.

Plate XXI

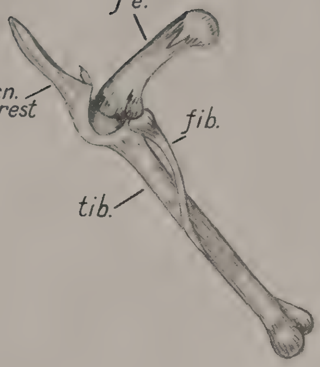


Fig. 46. *Colymbus glacialis* (after Owen).

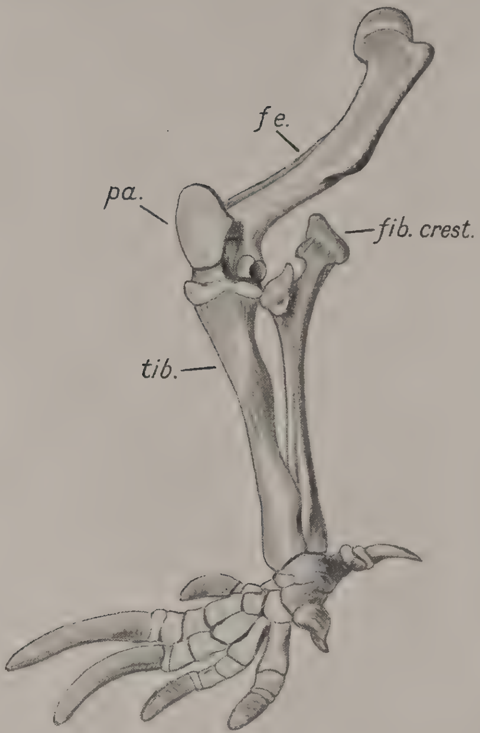


Fig. 47. *Echidna* (after Cuvier).

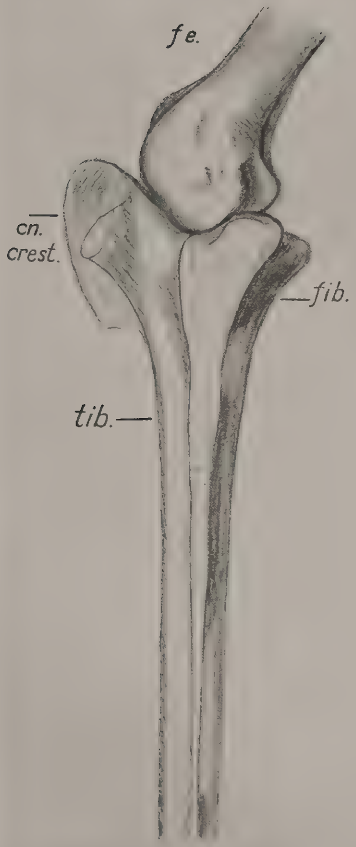


Fig. 48. Cereopsis Goose.

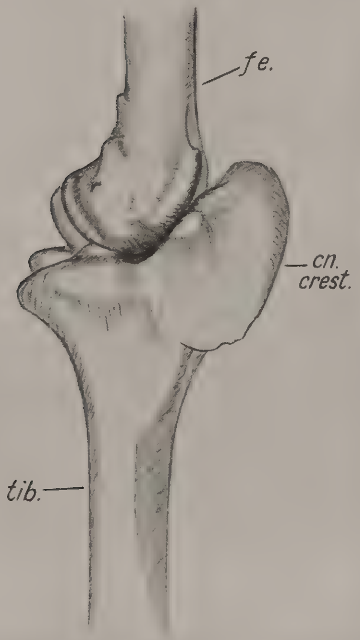


Fig. 49. Cereopsis Goose.

Plate XXII

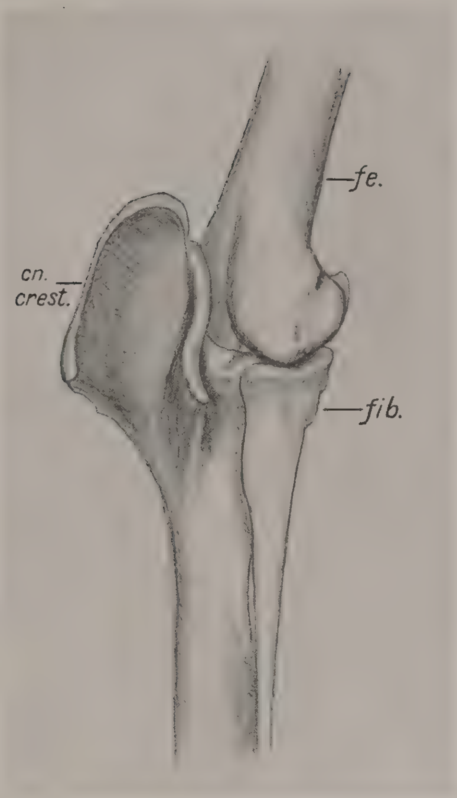


Fig. 50.

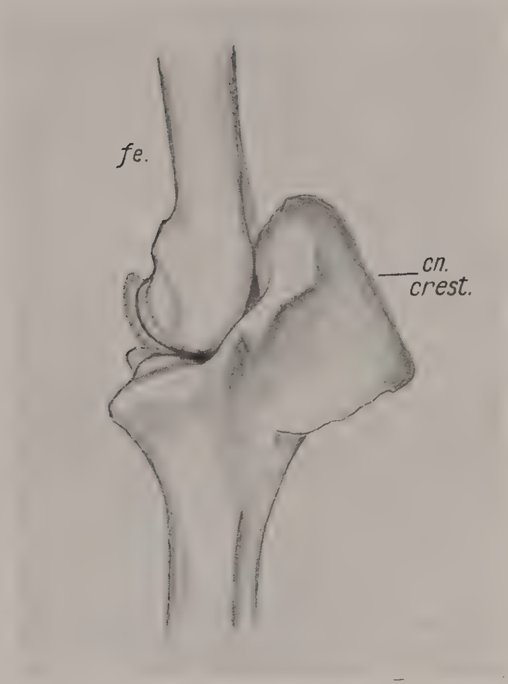


Fig. 51.

Albatross (*Diomedea exulans*).

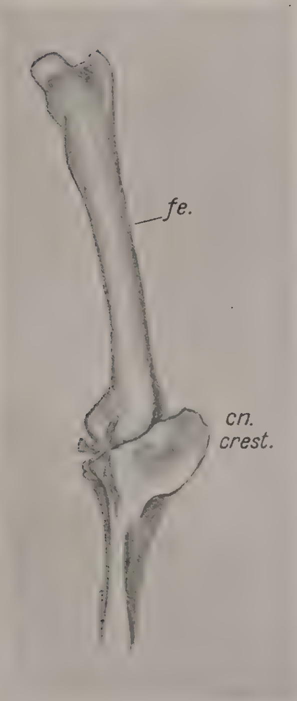


Fig. 52.

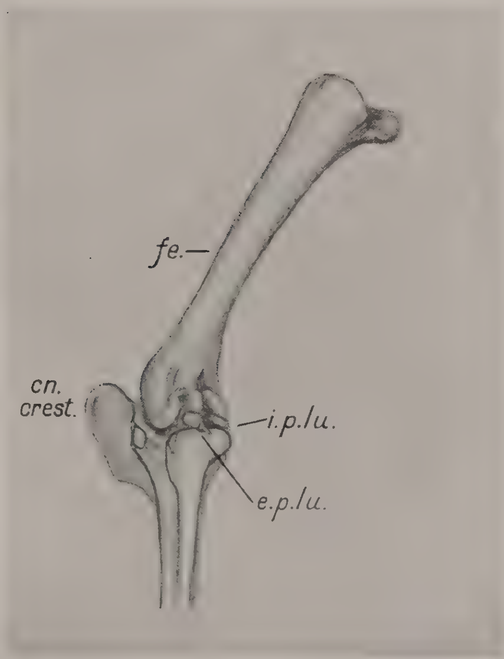


Fig. 53.

Dendrocygna.

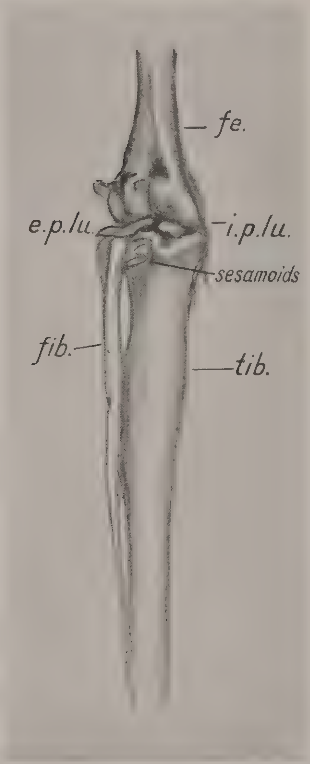


Fig. 54.

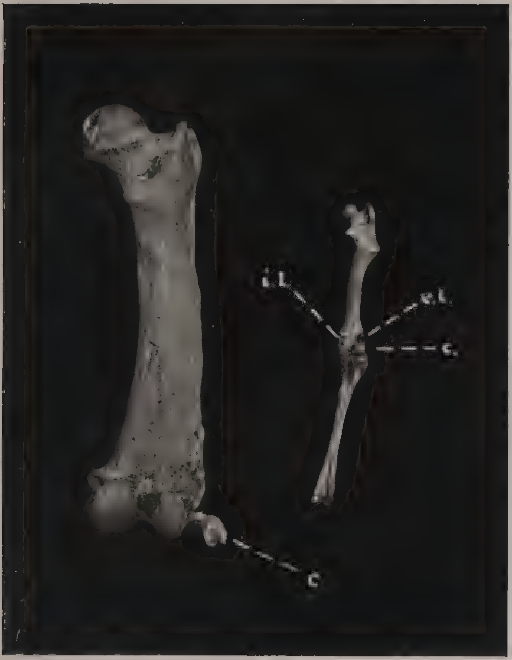


Fig. 55 *a*.
Tamandua Anteater
(*Tamandua tetradactyla*).

Fig. 55 *b*.
Common Squirrel
(*Sciurus vulgaris*).

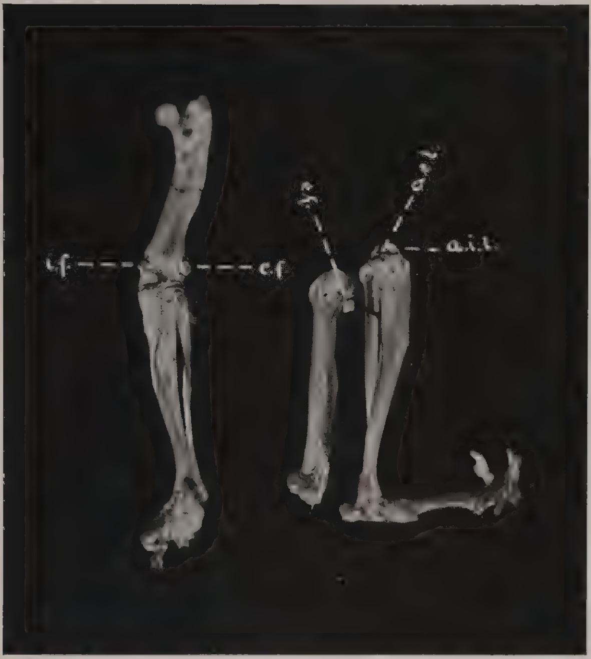


Fig. 56 *a*. Fig. 56 *b*.
Common Hedgehog (*Erinaceus europaeus*)
in two aspects.

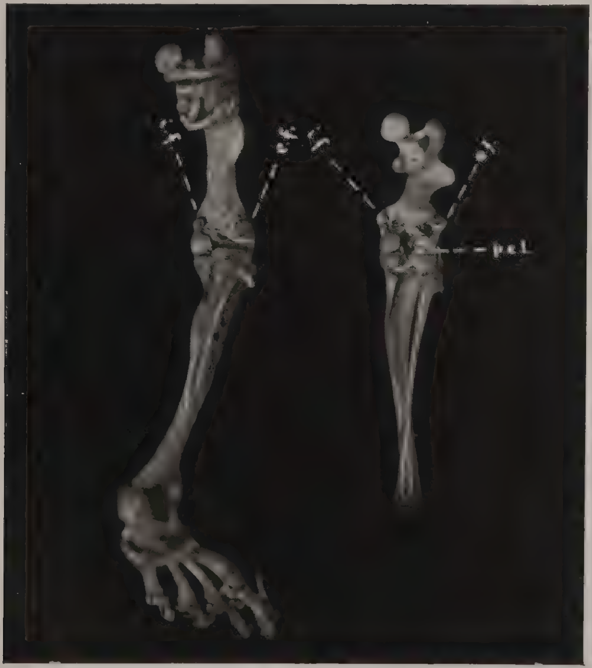


Fig. 57 *a*. Golden-bellied Rat
(*Hydromys chrysogaster*).

Fig. 57 *b*. Musquash
(*Fiber zibethicus*).

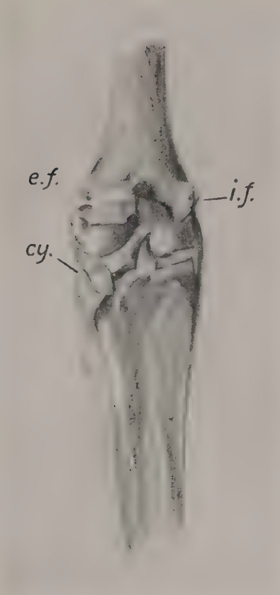


Fig. 58. Common rabbit (*Lepus cuniculus*).

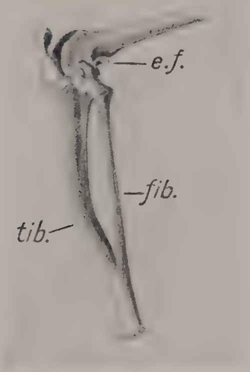


Fig. 59. *Potamogale velox* (West Africa).

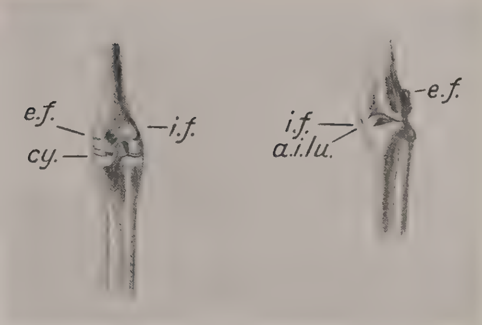


Fig. 60 *a*. Fig. 60 *b*.

Paraxerus jacksoni (African Squirrel).

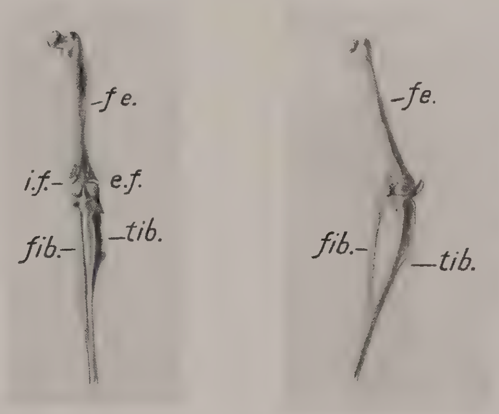


Fig. 62 *a*. Fig. 62 *b*.

Hylomys suillus dorsalis (Borneo).

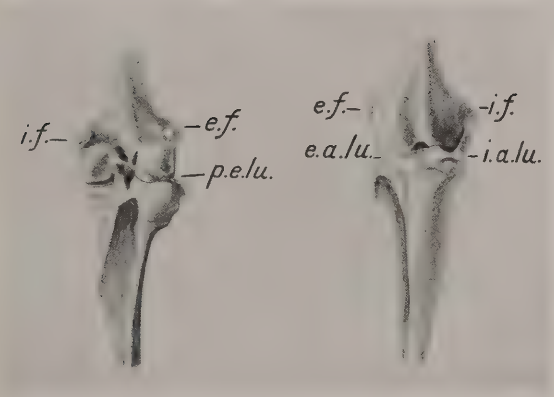


Fig. 61 *a*. Fig. 61 *b*.

Musquash (*Fiber zibethicus*).

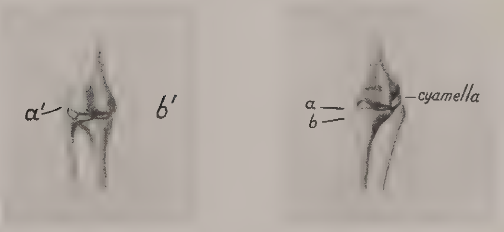


Fig. 63 *a*. Fig. 63 *b*.

Trachysaurus rugosus (Australian Lizard).

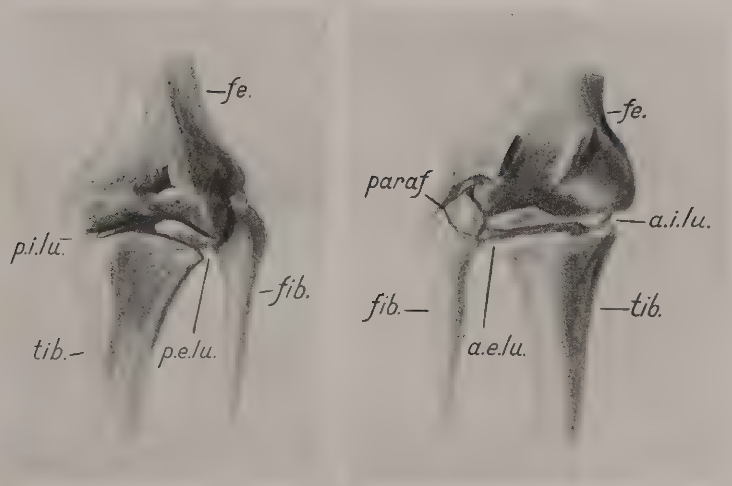


Fig. 64 *a*. Fig. 64 *b*.

Nile Monitor (*Varanus niloticus*).

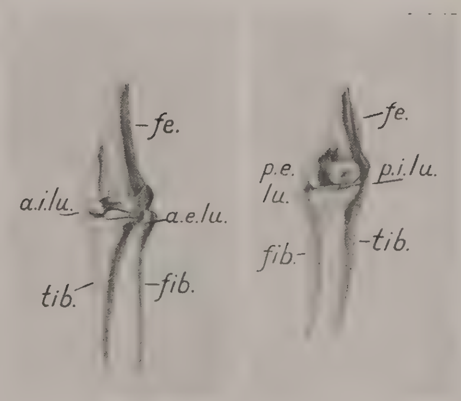


Fig. 65 *a*. Fig. 65 *b*.

Amphibolurus barbata.

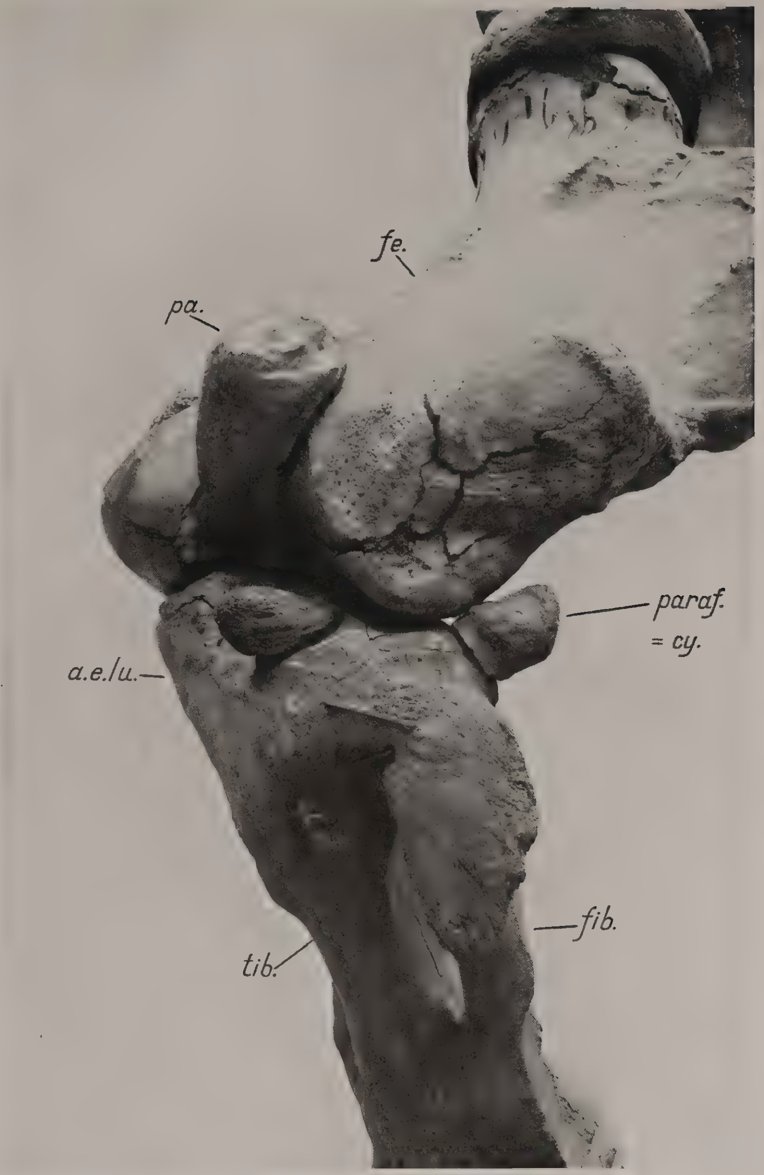


Fig. 66. Fossil Giant Sloth in R. C. of S.'s Museum (*Megatherium cuvieri*).

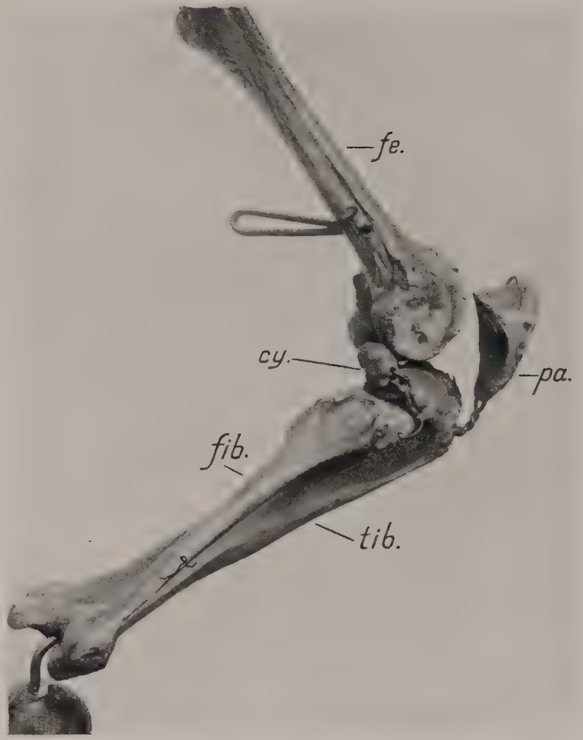


Fig. 67. Chinese Pangolin (*Manis aurita*).

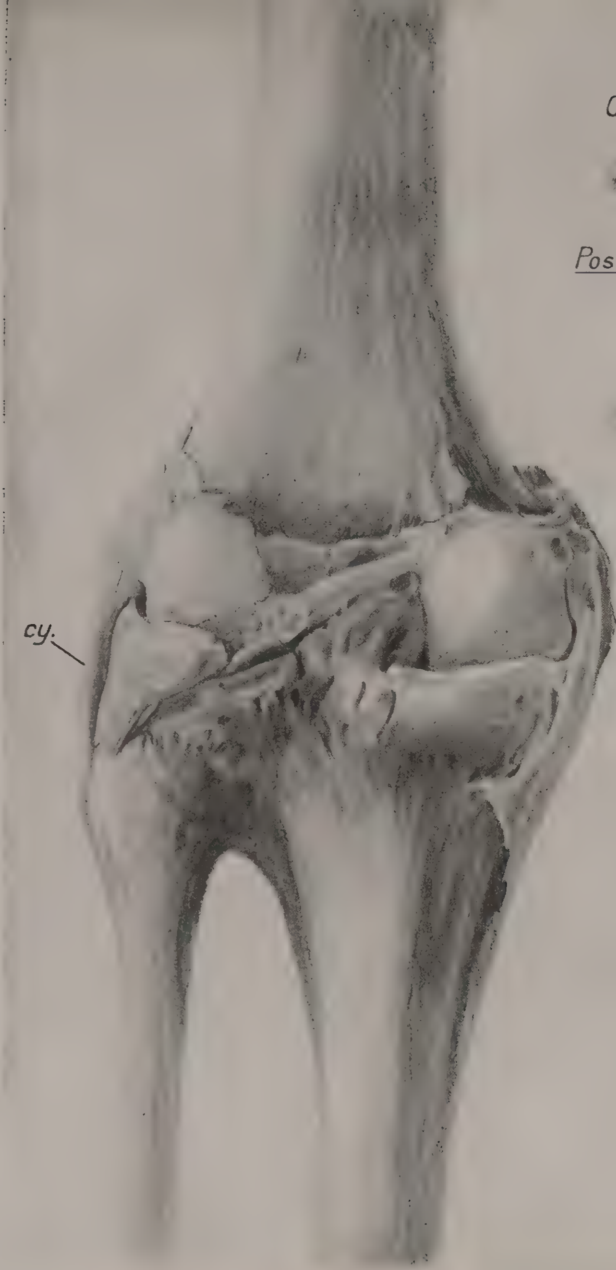
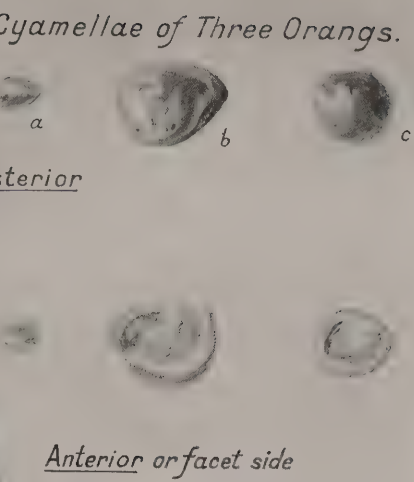


Fig. 68. Orang. Cyamella shown in position.



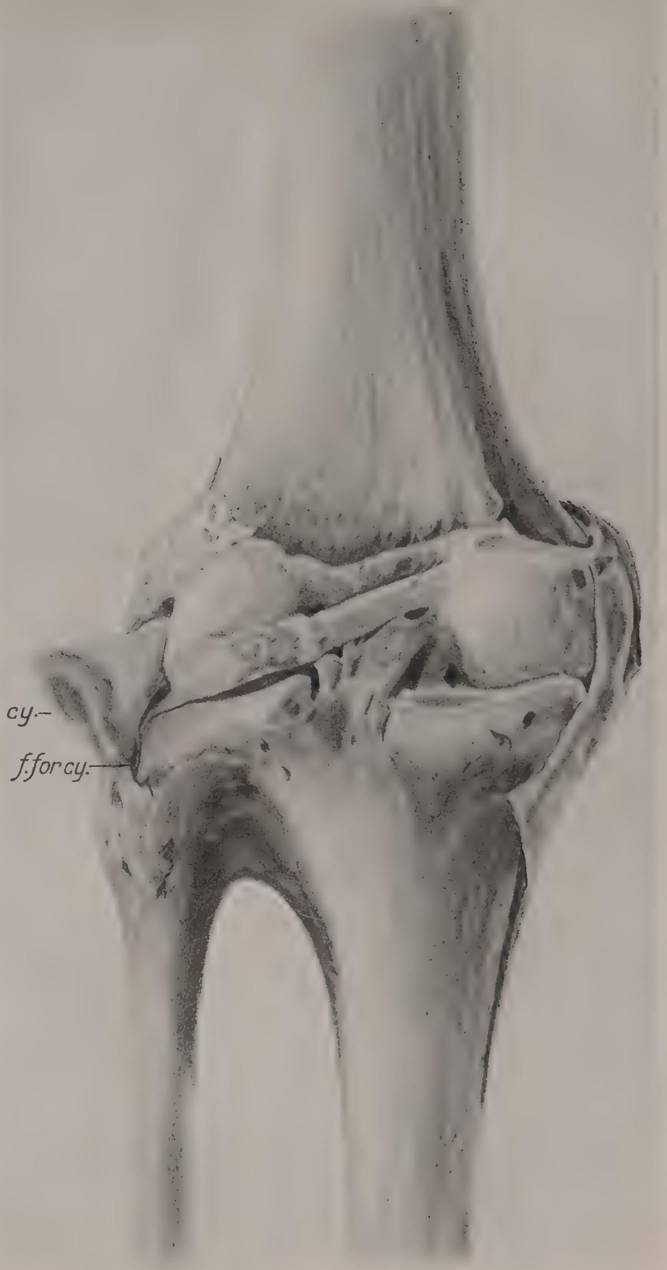


Fig. 69. Orang. Cyamella raised from its facet.

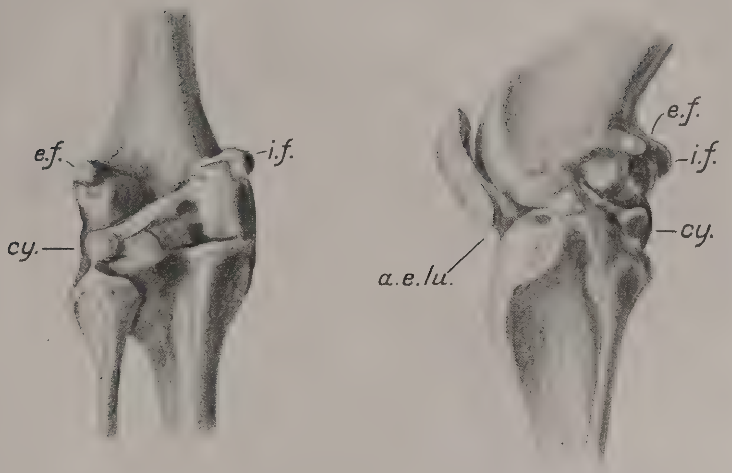


Fig. 70 *a*. Fig. 70 *b*.
Lemur varia in two aspects.

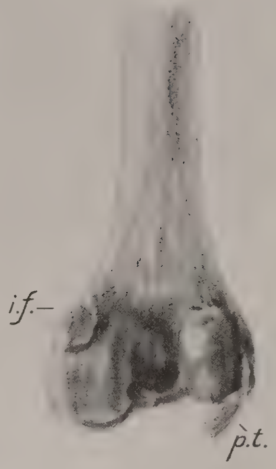


Fig. 72. Gibbon.

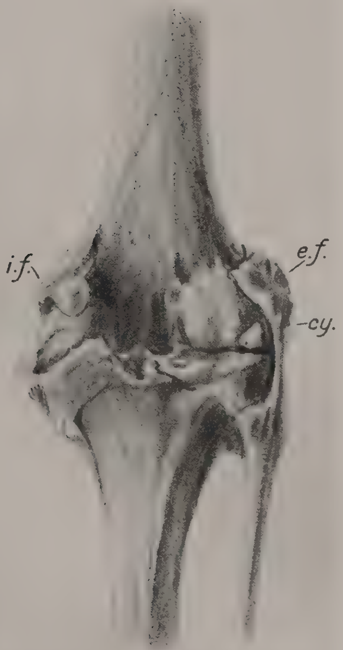


Fig. 71 *a*. *Mycetis palliatus*.

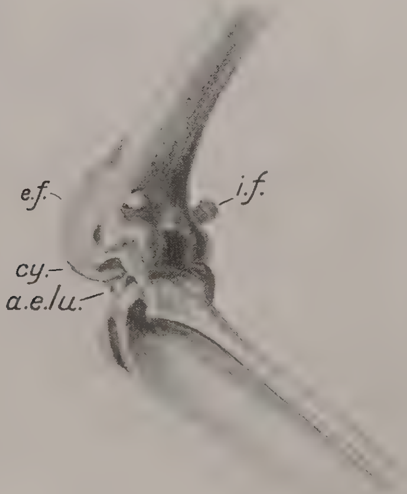


Fig. 73. *Lemur melanocephalus*.

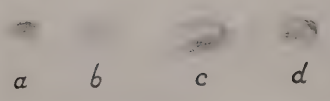


Fig. 71 *b*. *Mycetis palliatus*.

Plate XXVIII

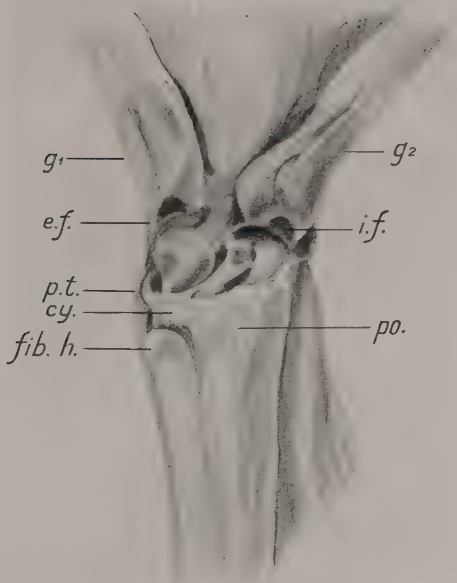


Fig. 74 *a*. Aye-Aye (*Chiromys*).

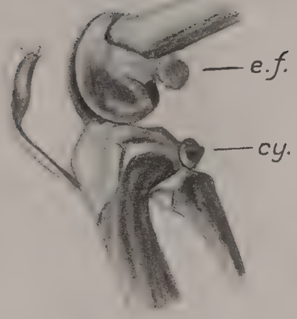


Fig. 74 *b*. *Chiromys* (after Owen).

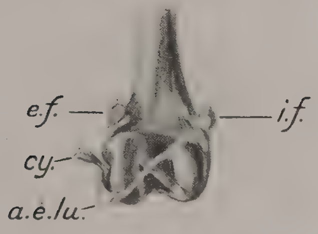


Fig. 75. *Lemur catta*.

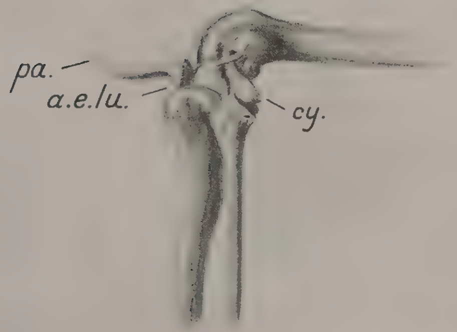


Fig. 76. *Perodicticus potto*.

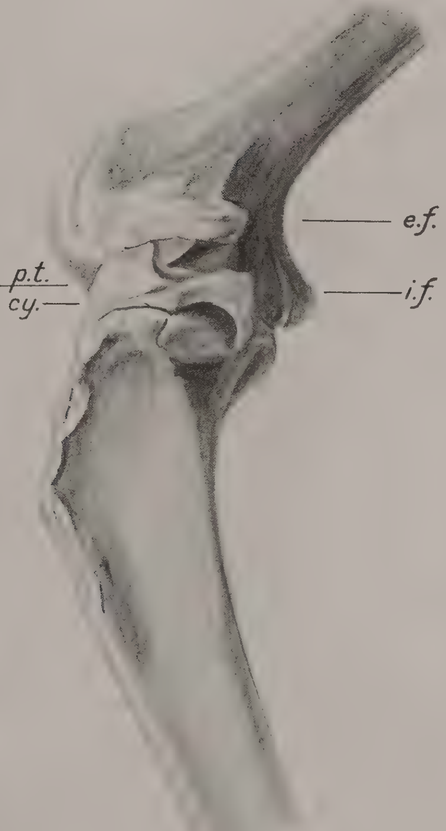


Fig. 77. *Indris brevicaudata*.

Plate XXIX

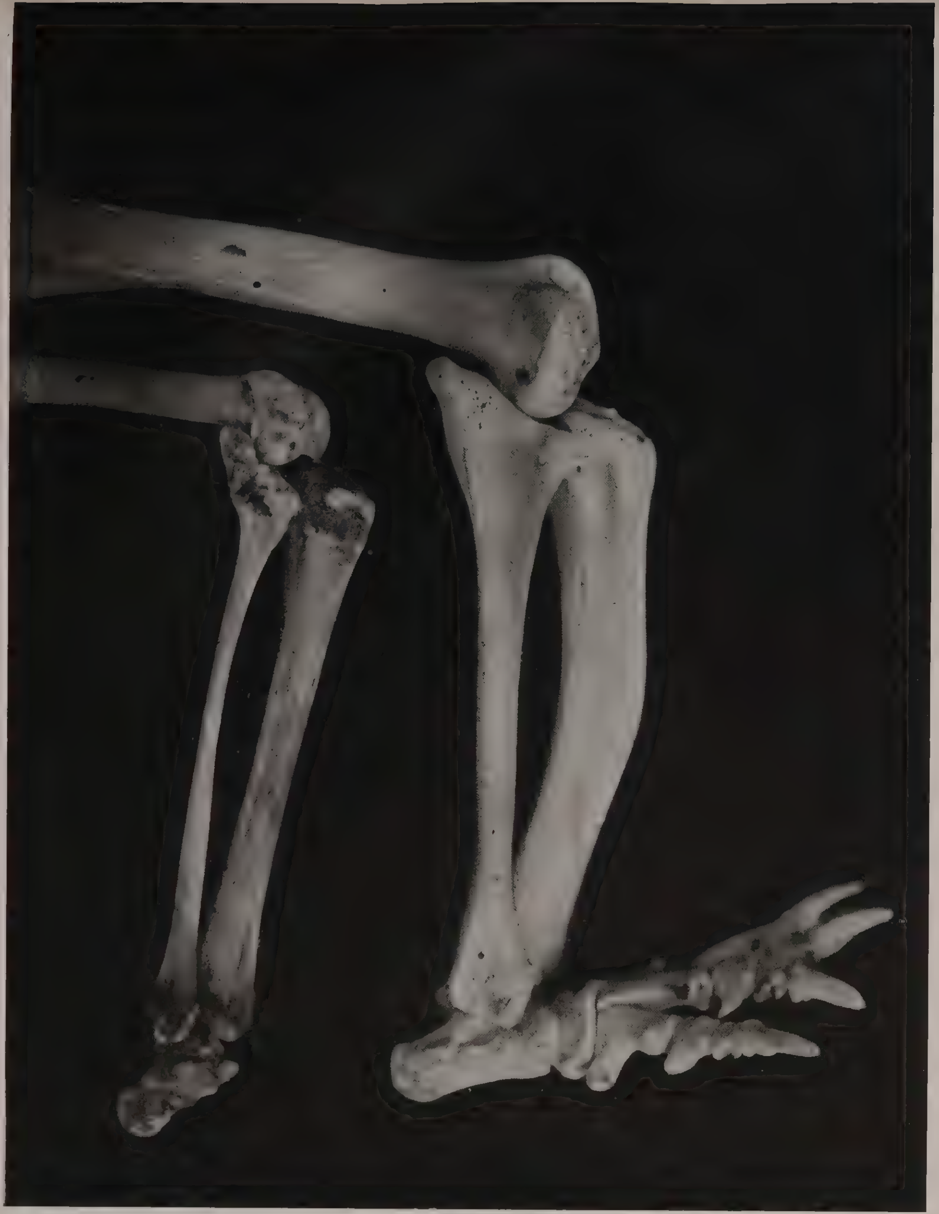


Fig. 78.

Tasmanian Devil (*Sarcophilus ursinus*).
Parafibula fused.

Wombat (*Phascolomys wombat*).
Parafibula fused.

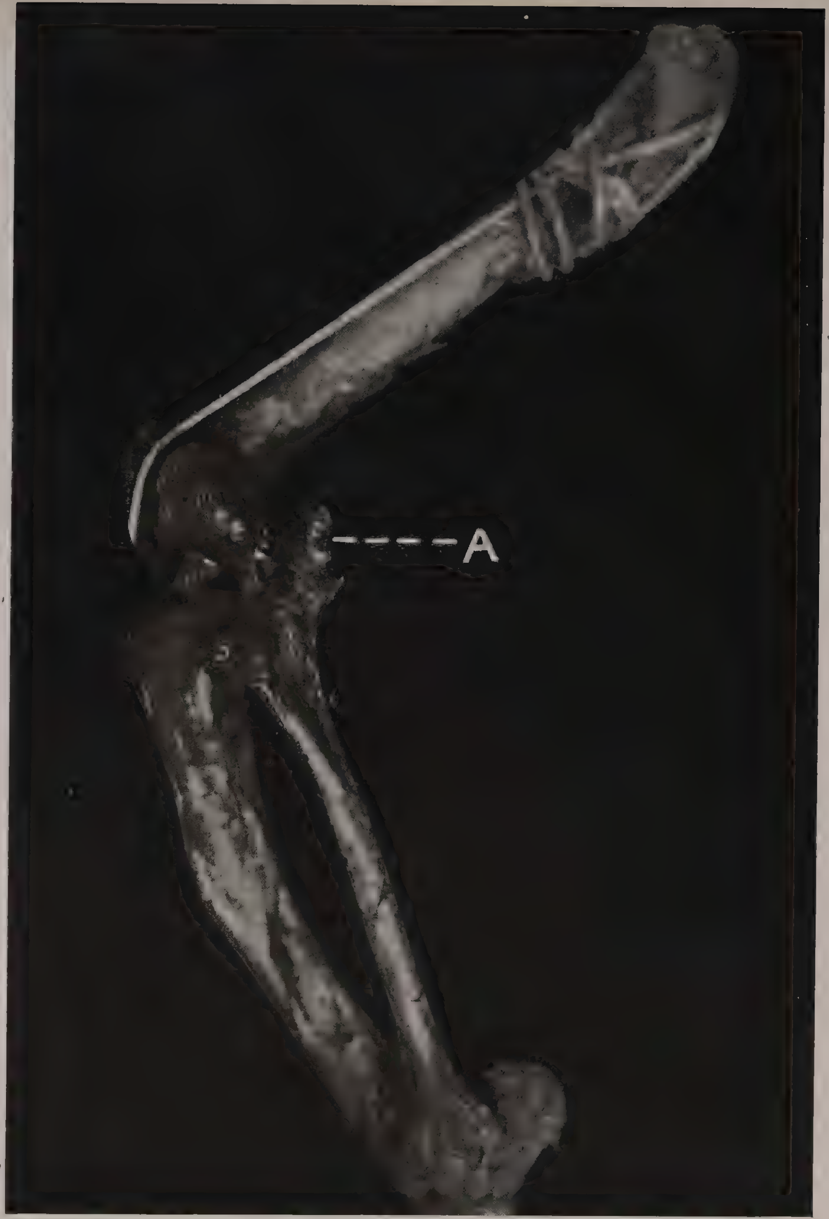


Fig. 79. Wombat. Parafibula free.

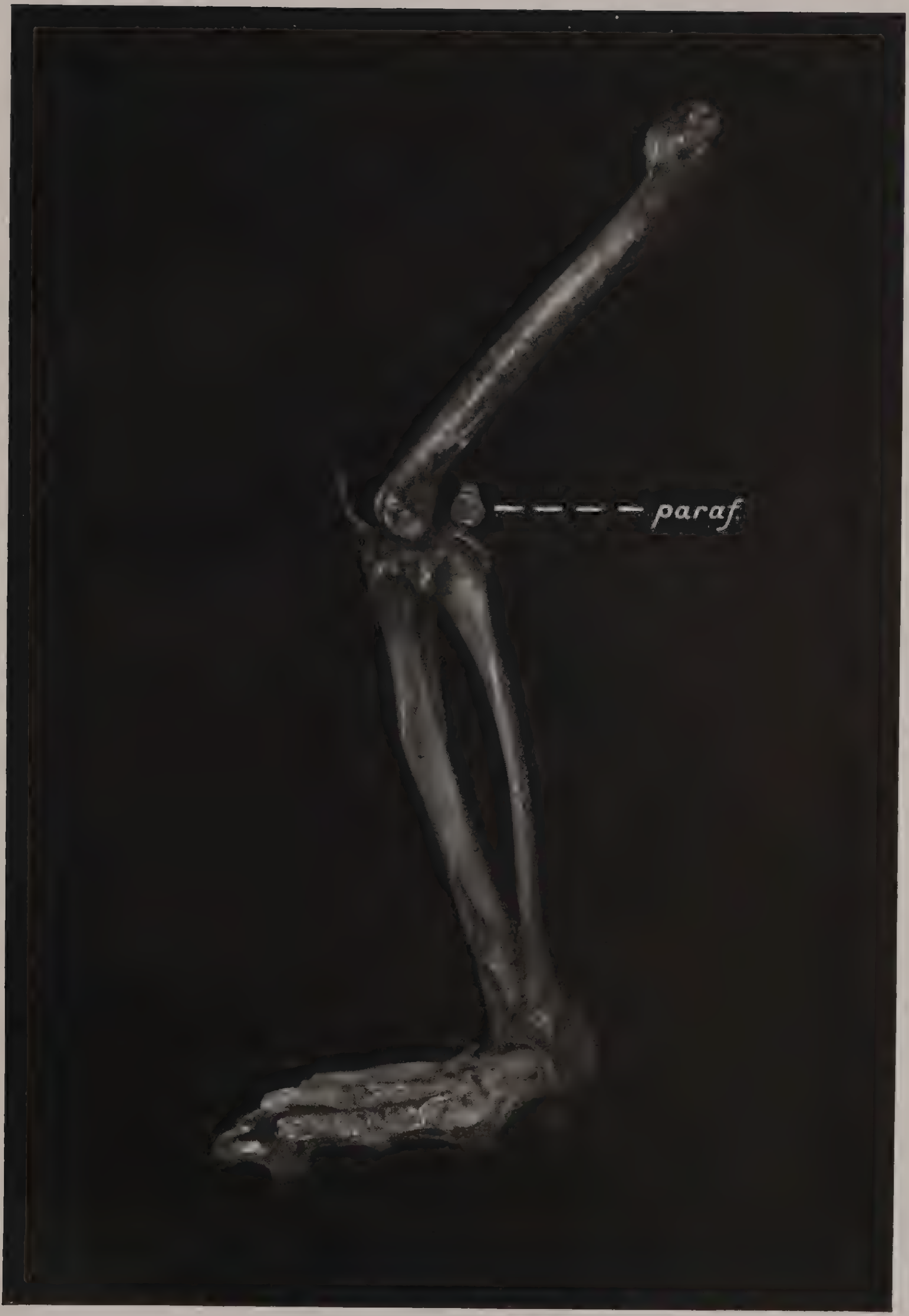


Fig. 80. *Phalangista vulpina.* Free parafibula.

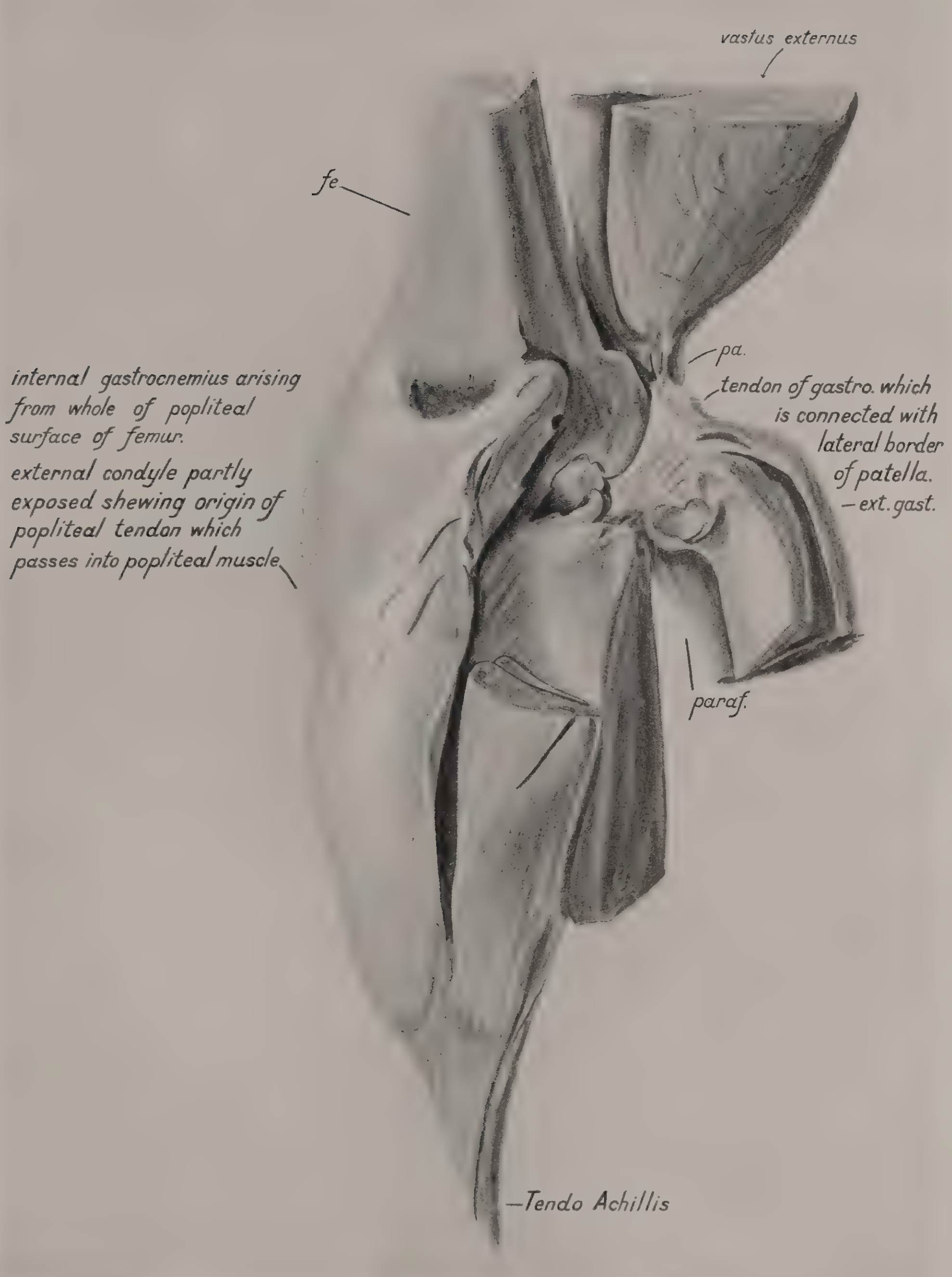

vastus externus
fe.
internal gastrocnemius arising from whole of popliteal surface of femur.
external condyle partly exposed shewing origin of popliteal tendon which passes into popliteal muscle
pa.
tendon of gastro. which is connected with lateral border of patella.
ext. gast.
paraf.
Tendo Achillis

Fig. 81. Knee-joint of *Phascolomys* (Wombat) with attached muscles.

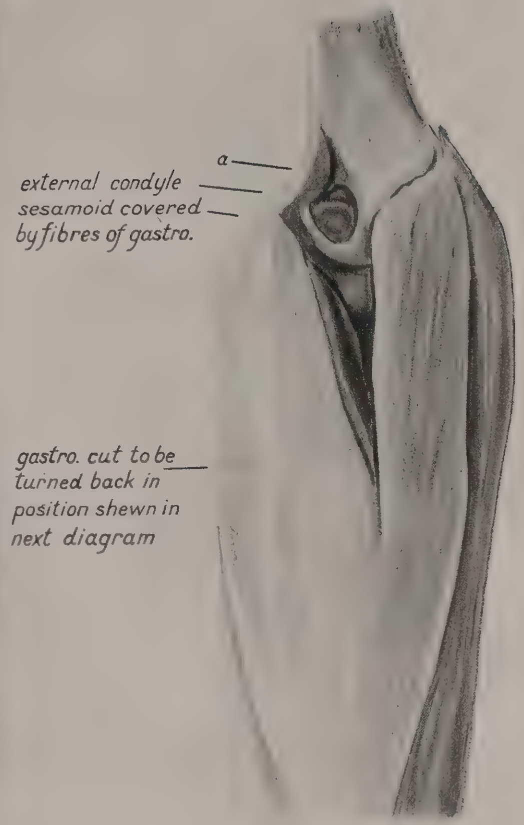

a
external condyle
sesamoid covered by fibres of gastro.
gastro. cut to be turned back in position shewn in next diagram

Fig. 82*a*.

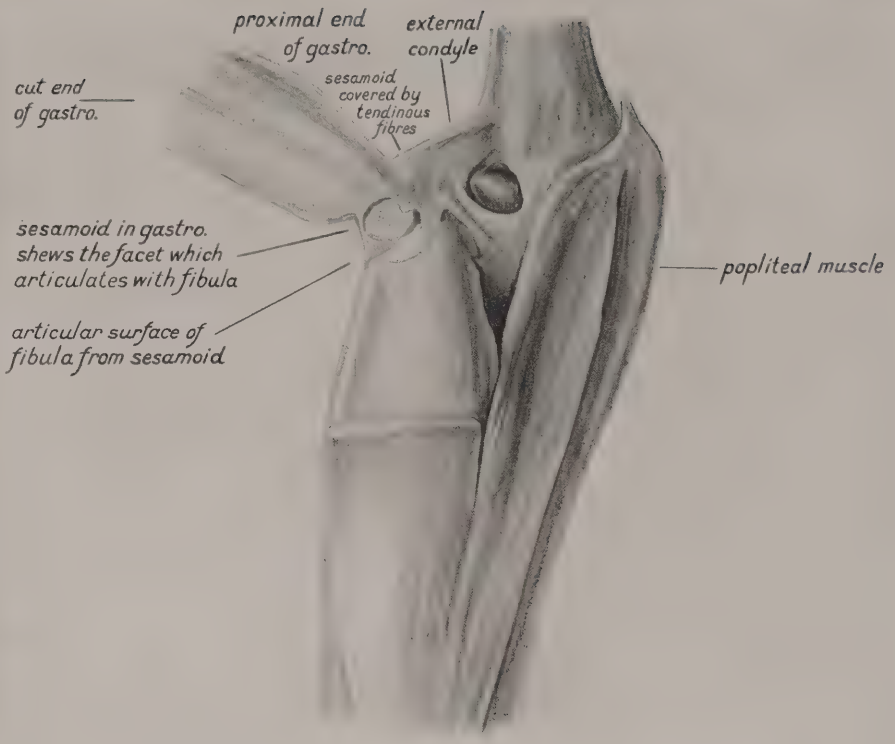

proximal end of gastro.
external condyle
cut end of gastro.
sesamoid covered by tendinous fibres
sesamoid in gastro. shews the facet which articulates with fibula
articular surface of fibula from sesamoid
popliteal muscle

Fig. 82 *b*.

Koala (*Phascolarctus cinereus*). Sesamoid articulating with fibula.

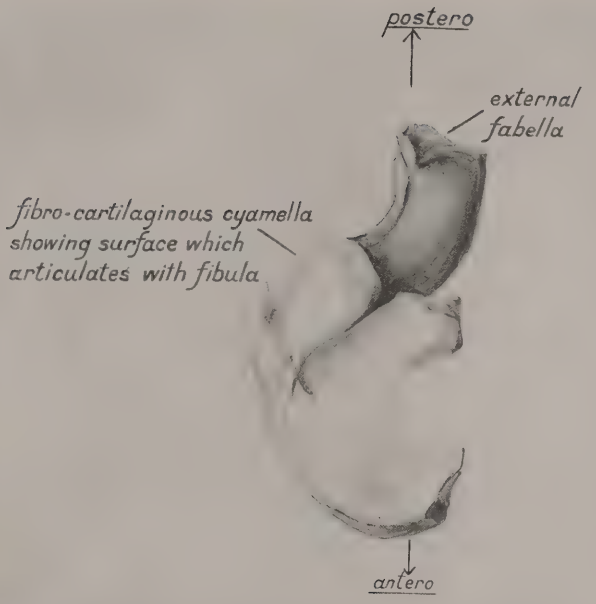

postero
external fabella
fibro-cartilaginous cyamella showing surface which articulates with fibula
antero

Fig. 83 *a*. *Macropus* sp.?

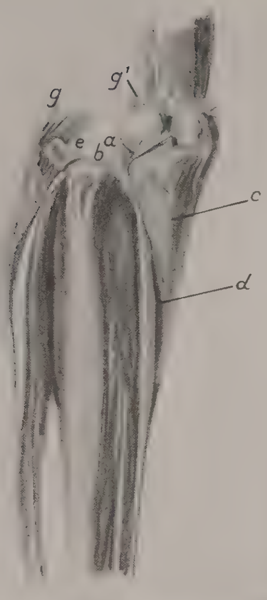


Fig. 84. Virginian Opossum (*Didelphys virginiana*).

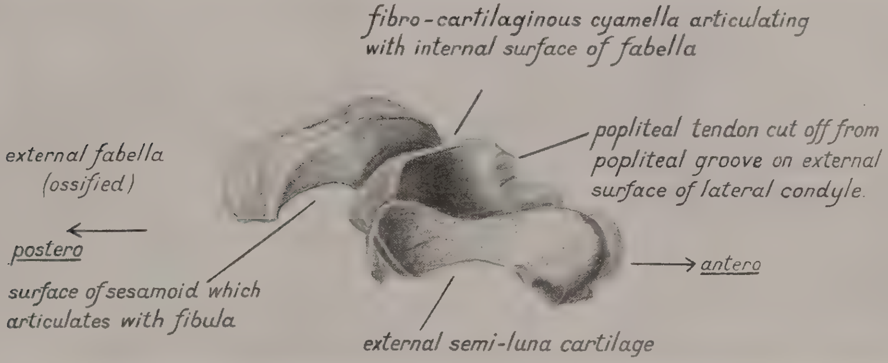

fibro-cartilaginous cyamella articulating with internal surface of fabella
popliteal tendon cut off from popliteal groove on external surface of lateral condyle.
external fabella (ossified)
postero
antero
surface of sesamoid which articulates with fibula
external semi-luna cartilage

Fig. 83 *b*. *Macropus* sp.?

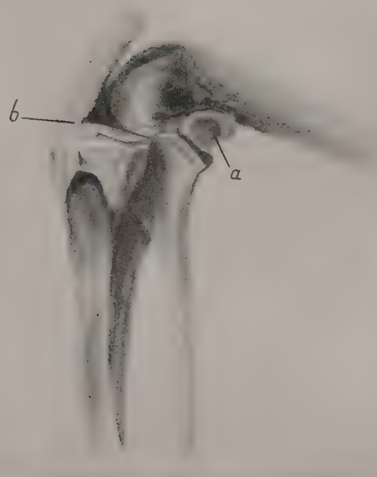


Fig. 85. *Phalangista vulpina*.

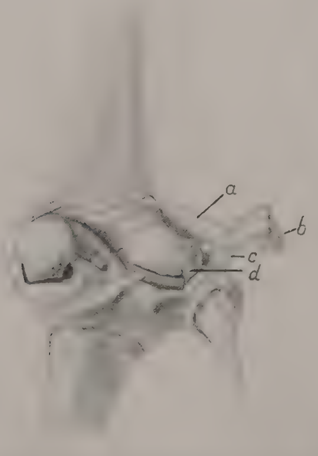


Fig. 86. Koala (*Phascolarctus cinereus*).

Plate XXXIV

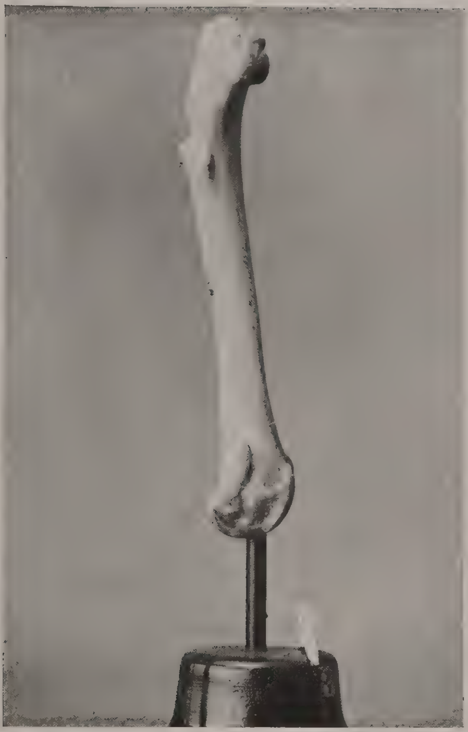


Fig. 87. Wallaby (*Macropus bennettii*).

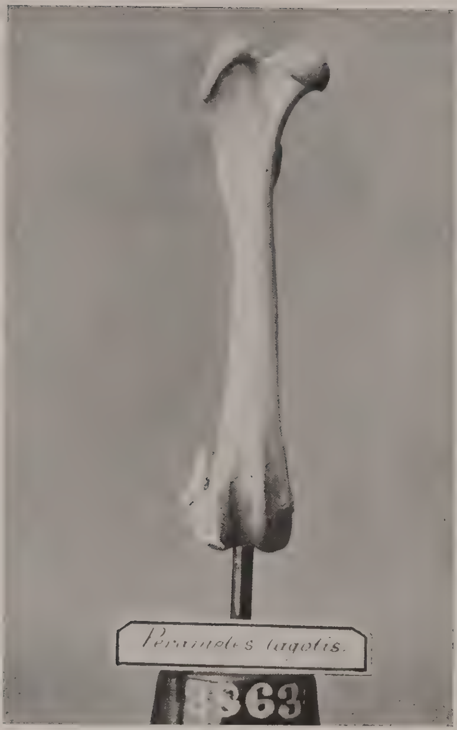


Fig. 88. Rabbit-eared Perameles.

Doubtful Position of Parafibula.

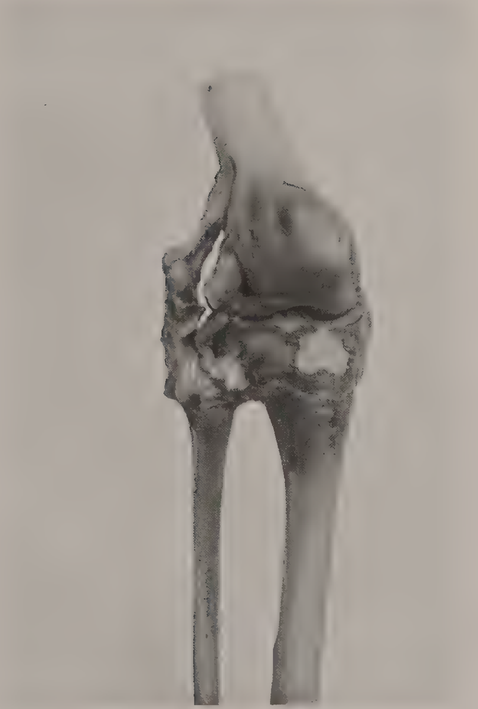


Fig. 89 *a*. Tasmanian Devil (*Sarcophilus ursinus*).
Anterior Aspect.

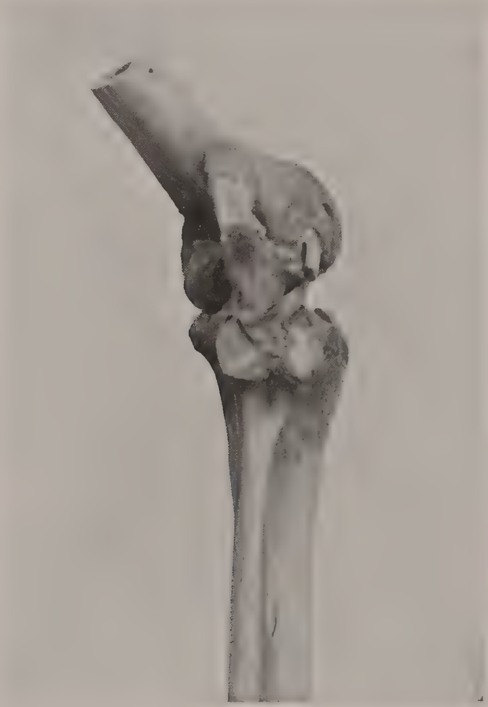


Fig. 89 *b*. Tasmanian Devil (*Sarcophilus ursinus*).
Lateral Aspect.

Correct Position of Parafibula.

Plate XXXV

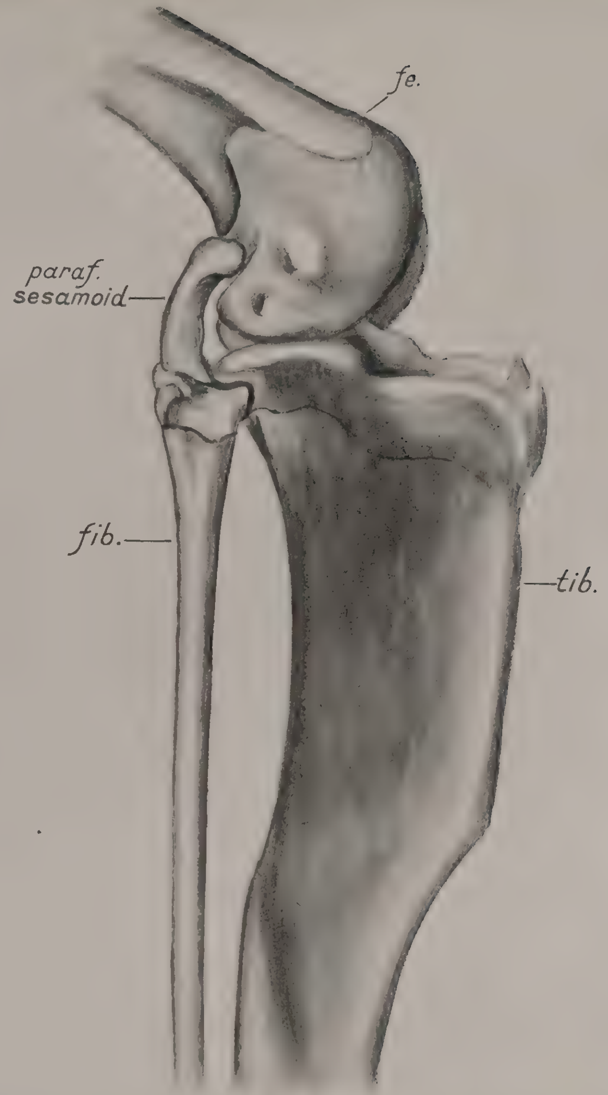


Fig. 90. Wallaby (*Halmaturus* sp.?).

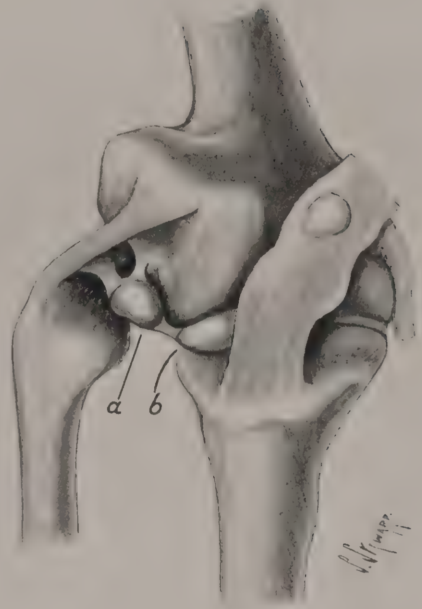


Fig. 91. *Corucia zebrata.* *a*, parafibular sesamoid; *b*, paratibial sesamoid united by ligament.

Plate XXXVI

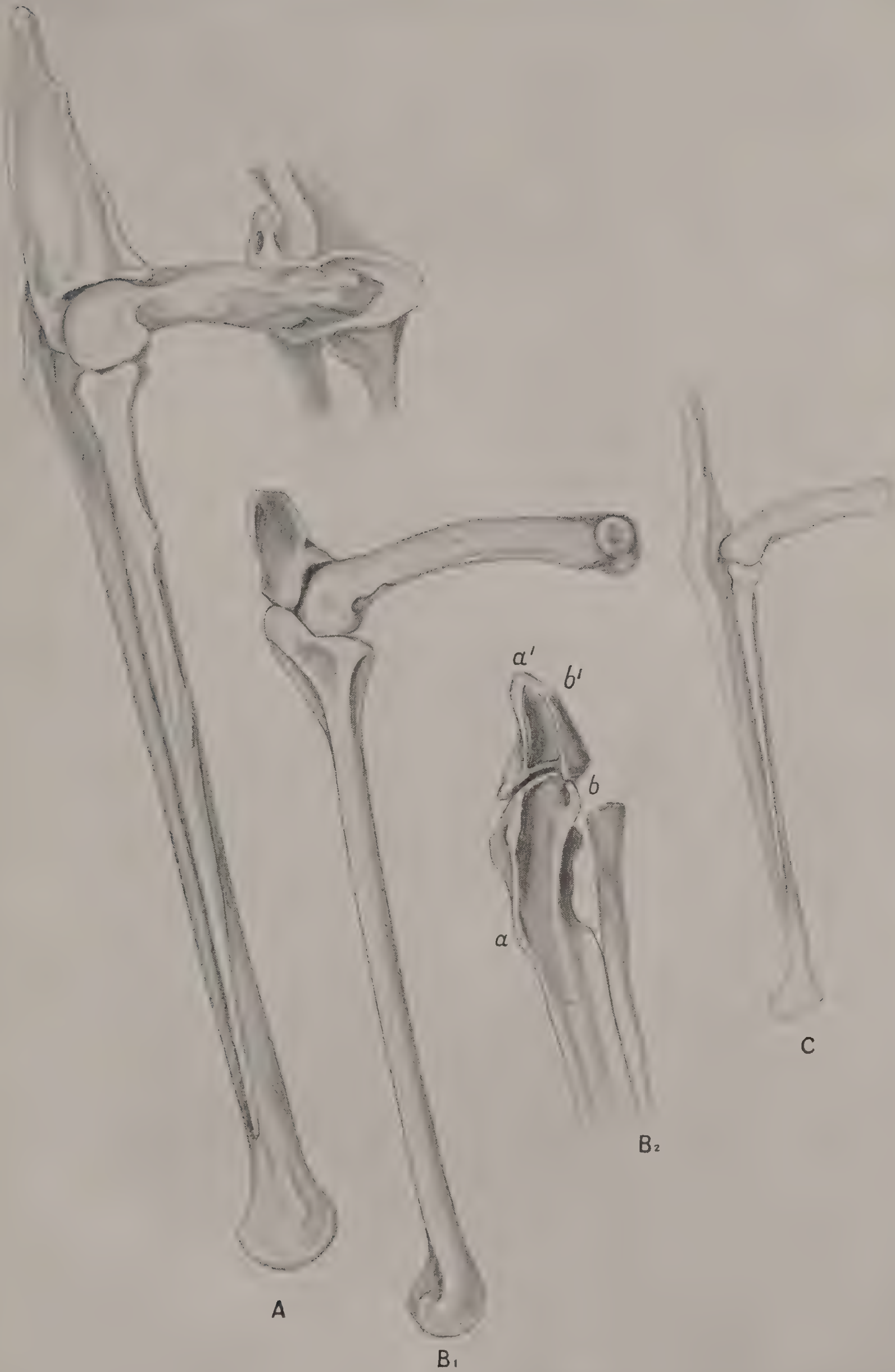


Fig. 92. Fig. 93 *a*. Fig. 93 *b*. Fig. 94.

A. *Hesperornis regalis*, after Marsh ($\frac{1}{2}$ natural size). **B_1.** R. Limb, mesial aspect from actual limb of Cormorant (natural size). **B_2.** L. Limb, lateral aspect from actual limb of Cormorant (natural size).
C. *Colymbus torquatus*, after Coues ($\frac{1}{2}$ natural size).

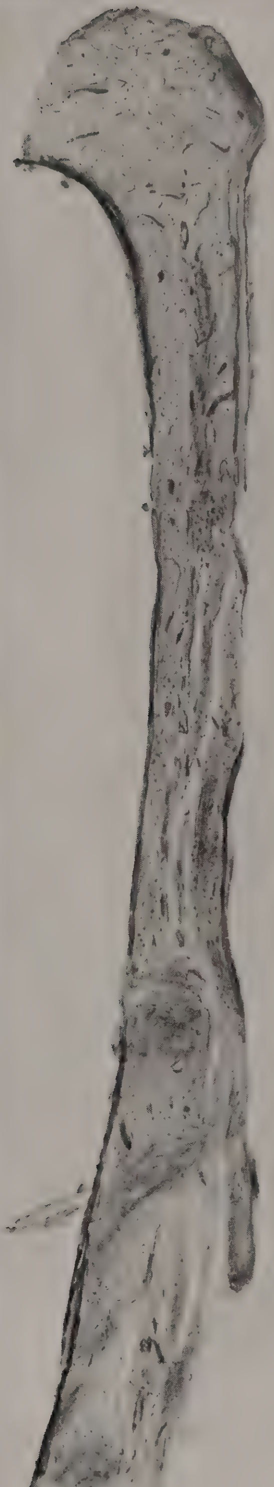


Fig. 95. Section of Fibular Crest of Young Platypus. × c. 60.

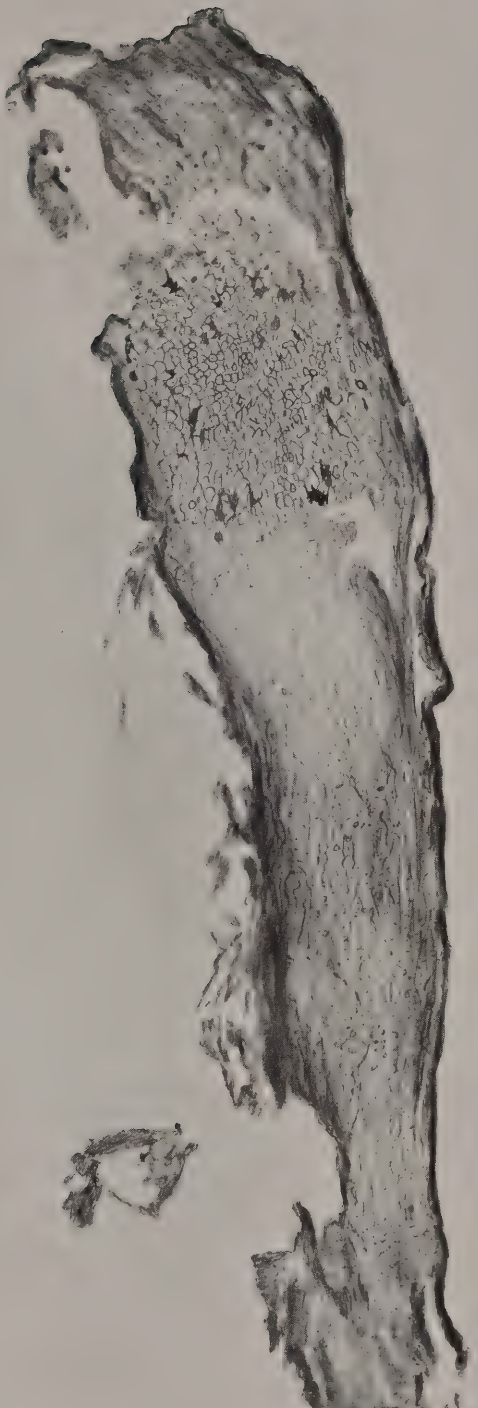


Fig. 96. Section of Fibular Crest of Embryo Platypus. × c. 60.

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